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AN ANALYSIS OF ARTHROPOD SUCCESSION IN CARRION AND THE EFFECT OF ITS DECOMPOSITION ON THE SOIL FAUNA

By G. F. BORNEMISSZA*

[Manuscript received August 16, 1956]

Summary

The present study falls into two clearly defined parts, one dealing with the succession of carrion-frequenting organisms in dead guinea pigs, the other examining the influence of carrion on the typical soil fauna of a sclerophyll woodland.

Five different stages of carcass decomposition were recognized and these were correlated with the animal communities occupying them. These communities were contrasted with the community dwelling in the leaf litter and soil.

The various stages of decomposition affected the underlying soil differently, the greatest effect being observed during the "black putrefaction" and "butyric fermentation" stages. During the black putrefaction stage, body fluids which passed into the soil formed a cemented crust with the plant litter and the upper soil layer. The liquified decomposition products during the butyric fermentation stage destroyed the underlying plants as well as the soil fauna.

The decomposition resulted in the production of two distinct zones in the upper soil layers which differed both physically and in arthropod populations from a control area. The fauna of the "carrion zone", i.e. the area beneath the carcass, differed greatly from that of the control area. The fauna of the "intermediate zone", i.e. the belt surrounding the carrion 10 cm wide, also showed substantial differences. Only carrion dwellers were present in the carrion zone, whereas both these and soil dwellers were present in the intermediate zone.

The decomposition of carrion had a marked effect on the soil fauna to a depth of 14 cm, but this was less drastic than in the upper soil layers.

The reinvasion of the carrion zone by soil arthropods was not completed after a year. At the end of the study period, subterranean forms were better re-established than soil-surface or litter dwellers.

I. INTRODUCTION

The fauna associated with the decomposing bodies of dead vertebrates has been studied from several viewpoints. Gleditsch (1752) (quoted by Pukowski 1933) described the role of the burying beetles (*Necrophorus* spp.). Both Melm (1755) and von Rosenhof (1761) (quoted also by Pukowski) also considered these beetles. More than a century later Megnin (1888) described the fauna of tombs. In a later work (1894) he gave a remarkably good account of the stages of decomposition of human corpses, and further, the succession of insect communities. Müller (1895) likewise investigated the insect fauna in corpses, while Dahl (1896) dealt with the carrion fauna similar to that of Megnin. Motter (1898) carried out observations on the fauna of graves (seen in reference only). In several works of Fabre (e.g. 1922) a number of observations or speculations can be found on carrion-dwelling beetles. Illingworth (1927) listed the carcass-visiting insects with particular emphasis on Diptera, while Pukowski (1933) reinvestigated the ecology and behaviour of

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Necrophorus spp. One of the most comprehensive studies on carrion and its fauna is that of Fuller (1934) who paid particular attention to blowflies. Waterhouse (1947) examined the relative importance of carrion and live sheep as breeding places for primary blowflies, and the significance of carrion as an environment for insect populations. Studies dealing with economic problems connected with blowflies (e.g. Holdaway 1930), however, are outside the scope of this work.

Kühnelt (1950) dealt with the decomposition of dead animals from a different point of view. He was interested in the contribution made by carrion and its fauna to soil formation. He showed that the various types of decomposition have a particular fauna associated with them. The normal soil fauna, where these processes are in progress, is reduced or changed in its composition.

The present observations deal both with carrion as an environment for animals and the effects of its decomposition on the soil fauna. The two different groups of decomposers are contrasted, and the role of the soil fauna in the decomposition of dead vertebrates is examined.

II. PROCEDURE

The investigation was carried out in King's Park, Perth, W.A., where the climate is of the Mediterranean type. The summer (December-March) is hot and dry and the winter (June-September) wet and cool, frosts being rare. Some rain falls during spring and autumn.

King's Park is a sclerophyll woodland approximately 1000 acres in extent. The flora consists of two associations. One is dominated by *Eucalyptus gomphocephala* D.C. (tauart) with a softer herbaceous undergrowth than in the other association. Shrubs commonly found in this association are *Pelargonium drummondii* Turcz., *Scaevola holosericea* De Vriese, *Jacksonia gracilis* Meissn., and the bush palm (*Macrozamia riedlei* (Fisch. ex Gaud.) C. A. Gardner). The other association is dominated by *Banksia* spp. and *E. marginata* Sm. (jarrah) which are accompanied by a prickly *Davesia* sp., *Oxylobium* sp., and other shrubs. Both communities occur on sandy soils.

The area chosen for the study (approximately 15 acres) was situated in the zone occupied by the tuart community where the sandy soil has a median particle diameter well below 0.5 mm (see Main and Carrigy 1953). Dead guinea pigs, averaging about 0.62 kg in weight, were used as carrion. These were put out during the spring when the stages of decomposition were most easily recognized, and the arthropod fauna was most varied and abundant.

For the study of the succession of carrion-visiting arthropods a special trap (Fig. 1) was designed. The animals trapped in two of these funnels were collected in jars filled with 96 per cent. alcohol. These were changed daily for the first 21 days, every second day from 21-30 days, and every third day between 30 and 40 days. This method showed the order in which animals appeared on the carcasses and their absolute abundance. The traps, however, were not suitable for collection of all the flies or parasitic Hymenoptera (which were not required). As the carcass in the trap was suspended on a wide-mesh wire, the rate at which it dried out was slightly higher than at ground level. Consequently the time-table in Figure 2 has been

corrected by reference to carcasses placed on the ground and used also for the study of soil arthropods. Supplementary observations on carrion-visiting arthropods were also made on the latter (e.g. see Table 1).

In order to study the effects of the decomposition of carrion on the soil fauna, guinea pig carcasses were placed on the ground. Soil samples with a surface area of 43 sq. cm and a depth of 3.5 cm were collected from beneath the carrion and at distances of 10, 20, and 40 cm from it by means of a cylindrical tin. The samples

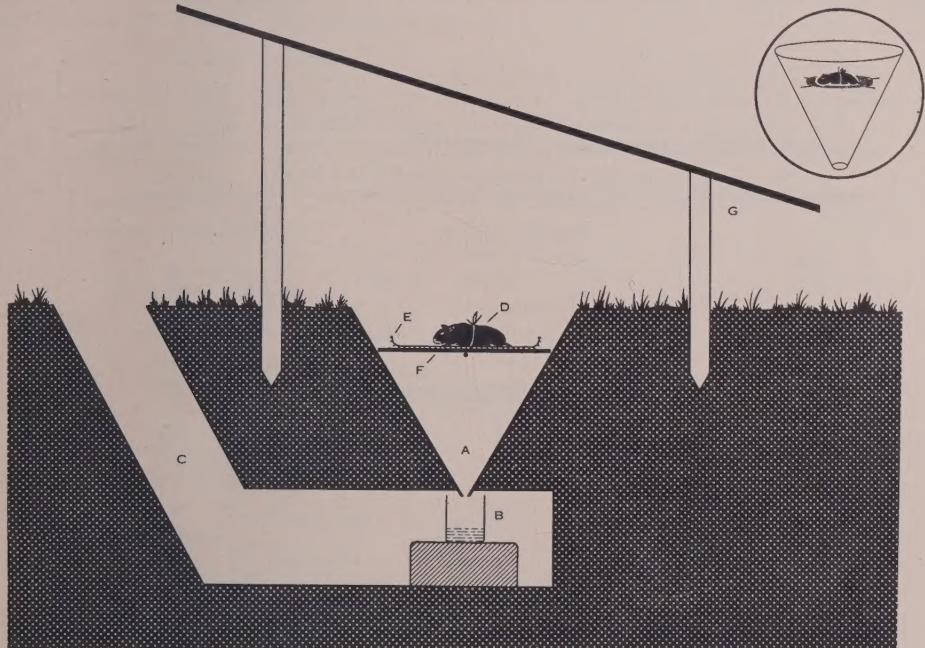


Fig. 1.—Trap used to capture the carrion-visiting arthropods. Top of funnel (A, dia. 45 cm) is flush with soil surface. Animals were collected in jars B which were changed at various intervals through pipe C, the entrance being covered while the trap was operating. The carcass D was placed on a wide-mesh wire screen E suspended on cross-wires F in the funnel. The iron G served to keep rain off the funnel.

taken at 40 cm served as controls. Further samplings were carried out to a depth of 15 cm, the surface area in this case being 25 sq. cm. These latter samples were dissected into their natural layers (e.g. A₀, A₁, A₂, etc.). Five carcasses were sampled once for three stages of carrion decomposition at the distances and depths mentioned. The soil arthropods were extracted from the samples by modified Berlese funnels.

III. THE CARRION FAUNA

(a) *Stages of Carrion Decomposition*

The number of stages of decomposition which can be observed in a decaying vertebrate carcass is largely dependent on climatic and seasonal conditions. The type of soil has a modifying influence which must also be taken into account.

In the present study five stages were recognized:

- (i) "*Initial Decay*" Stage.—0-2 days. The carcass appears fresh externally. Decomposition begins internally through the activities of bacteria—probably also protozoa and nematodes—present in the animal before death.
- (ii) "*Putrefaction*" Stage.—2-12 days. The carrion is swollen by gas produced internally; a distinct odour of putrefying flesh is apparent.

TABLE 1

NUMBERS OF CARRION-FREQUENTING ARTHROPODS EXTRACTED FROM SOIL SAMPLES DURING THREE STAGES OF DECOMPOSITION

No carrion dwellers were recovered from soil samples from the control zone. Values are the means for 10 samples (area 43 sq. cm)

Groups of Animals	Beneath Carrion			10 cm from Carrion		
	Black Putrefaction Stage	Butyric Fermentation Stage	Dry Decay Stage	Black Putrefaction Stage	Butyric Fermentation Stage	Dry Decay Stage
Staphylinid adults	16.3	2.2	—	0.9	0.1	—
Staphylinid larvae	13.0	14.8	—	0.1	1.5	—
Histerid adults	3.5	1.5	—	0.5	0.2	—
Histerid larvae	2.4	0.2	—	1.9	0.1	—
Dermestid adults	—	0.1	—	—	—	—
Dermestid larvae	—	0.6	—	0.3	0.1	—
Trichopterygid adults	79.2	48.8	—	0.2	1.9	—
Trichopterygid larvae	—	1.8	—	—	0.5	—
Ptinidae	—	0.2	—	—	—	—
Tineid larvae	—	0.4	2.9	—	2.1	0.1
Parasitic Hymenoptera	—	—	—	—	0.1	—
Dipterous larvae	8.3	3.5	—	—	0.1	—
Gamasidae	209.0	355.1	2.4	190.0	93.3	1.9
Tyroglyphidae	35.6	419.2	1077.4	2.4	74.7	72.0

- (iii) "*Black Putrefaction*" Stage.—12-20 days. The flesh becomes creamy in consistency, exposed parts being black. At the beginning of this stage the swollen body collapses after the escape of gases. The odour of decay is very strong.

- (iv) "*Butyric Fermentation*" Stage.—20-40 days. The carcass is drying out. During the first half of this stage, while some flesh remains, the characteristic cheesy odour of butyric acid is present. This stage is so named because Kühnelt called this kind of decomposition "Buttersäuregarung". The ventral surface of carrion is covered by mould, suggesting that some fermentation is occurring.

(v) "Dry Decay" Stage.—40–450 days. The carcass is almost dry and decays very slowly. Between 300 and 450 days the remains of the hair disappear leaving the bones only.

The time intervals indicated above are approximate. Weather conditions and differences in the microclimate, depending on the position of the carcasses relative to trees and shrubs, obviously influenced the rate of decay, e.g. carcasses shaded by shrubs and trees for several hours per day were occupied by species different from those in the unshaded carcasses.

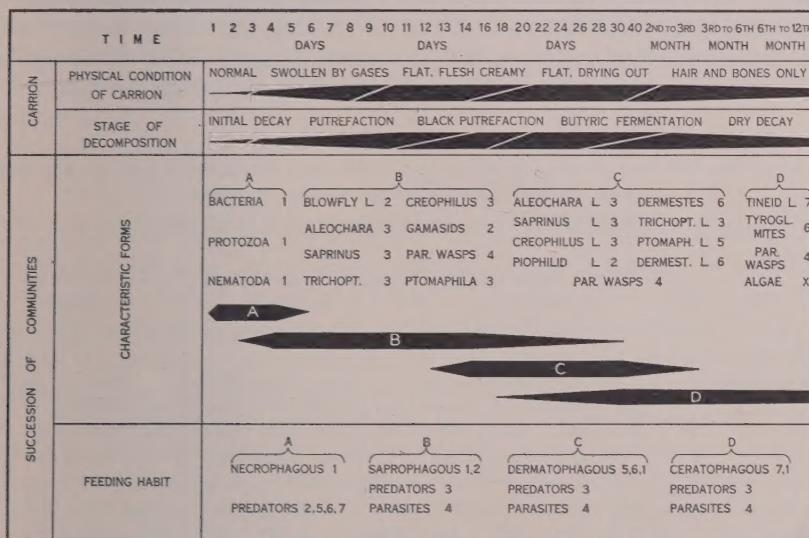


Fig. 2.—Diagram illustrating the succession of communities visiting carrion. Variations in the width of each band indicate approximately the relative activity of each community at different times. Numbers beside characteristic forms refer to the feeding habit (see bottom part of diagram) of each group respectively. Further explanation in text.

(b) Observations on the Succession

Figure 2 shows the results of the present investigation on the successional aspects of this fauna. Each community occupied the carrion at a particular stage of decomposition and may be named after the feeding habit of its characteristic members. The "necrophagous" community, i.e. that present when the carcass is in the initial decay stage, is composed of bacteria, protozoa, and nematoda. Although these organisms were not studied, they have to be included in any consideration of succession. The histogram A (Fig. 2) representing this community, with the probable variations in specific composition in the subsequent stages, is suggestive only. The predators of these groups include all those animals (e.g. fly larvae, *Ptomaphila* and *Dermestes* larvae, etc.) which feed on carrion, consuming the members of this community with their food.

The term "saprophagous" is used for community B. It is realized that the words "necrophagous" and "saprophagous" have similar meanings. It seems

necessary, however, to differentiate the initial decay stage from that of putrefaction and black putrefaction which followed when bacterial activity increased. Further, community *B* includes probably two distinct communities according to the kind of decomposition, but owing to taxonomic difficulties their separation was impossible to carry out. The saprophagous community was characterized at first by the presence of the primary blowfly larvae (*Lucilia cuprina* Wied. and *Calliphora australis* Boisd.), later by gamasid mites, and flies like *Peronia* and *Sarcophaga* spp. The principal predators were *Creophilus erythrocephalus* Fabr. (fam. Staphylinidae) and *Ptomaphila lachrymosa* Schr. (fam. Silphidae) together with various species of *Aleochara* (fam. Staphylinidae) and *Saprinus* (fam. Histeridae) feeding on blowfly larvae, and the numerous trichopterygid beetles probably attacking gamasid mites. Entomophagous parasites included Pteromalidae, Diapriidae, Chalcididae, and Encyrtidae.

TABLE 2

HORIZONTAL DISTRIBUTION OF SOIL ARTHROPODS (OTHER THAN COLLEMBOLA AND ACARI) BENEATH
AND AT DIFFERENT DISTANCES FROM CARRION
Values are the means for 10 samples (area 43 sq. cm)

Groups of Arthropods	Black Putrefaction Stage				Butyric Fermentation Stage				Dry Decay Stage			
	Control	Be- neath Car- rion	10 cm from Car- rion	20 cm from Car- rion	Control	Be- neath Car- rion	10 cm from Car- rion	20 cm from Car- rion	Control	Be- neath Car- rion	10 cm from Car- rion	20 cm from Car- rion
Pauropoda	0.6	0.2	1.0	0.9	1.2	—	1.2	1.4	4.9	0.9	11.0	11.8
Sympyla	3.8	2.1	5.3	3.3	2.2	—	2.9	0.7	3.8	1.3	4.4	3.6
Protura	1.0	1.8	—	0.6	0.5	—	0.1	0.8	0.8	4.8	2.9	2.1
<i>Plectochetos</i> <i>longissimus</i>	3.0	0.5	1.6	1.1	0.9	—	0.2	0.6	3.0	0.2	1.6	1.1
Pseudoscorpiones	3.8	1.2	2.7	2.9	1.6	—	0.6	1.0	2.0	—	4.0	0.9

The "dermatophagous community" of the succession was characterized by the skin and ligament feeders, and was present during the butyric fermentation stage of decomposition. The characteristic forms on most carcasses were the larvae of the cheese fly *Piophila casei* L. feeding on the remains of the flesh. Towards the end of this stage *P. lachrymosa* larvae were most typical on moist carrion whereas adults and larvae of *Dermestes vulpinus* Fabr. and *Necrobia rufipes* De Geer (Cleridae) were typical on dry or rapidly-drying carcasses. The principal predators were staphylinid and histerid larvae. Entomophagous parasites were represented by the hymenopterous families listed above.

Before the carrion had dried out completely, larvae of an unidentified tineid moth were very apparent feeding on hair (see Table 1 and Fig. 2). These typified the "ceratophagous community" of the succession. The larvae were present from the 16th to the 350th day, i.e. as long as hair was present. Where any skin was left by the skin feeders of the previous stage, an immense number of tyroglyphid mites

(see Table 1) consumed the remainder leaving nothing but bones. During the wet winter and moist spring the bones were covered by algae (*Cyanophyceae*). Entomophagous parasites and predators were very scarce in this community. The latter were represented by a few staphylinid larvae and small adult carabids and staphylinids.

The carrion fauna which appeared in the leaf litter and the upper layer of soil was extracted from soil samples (Table 1) collected beneath the carcass, and 10 cm away from it, during the last three stages of decomposition. Differences were most obvious between the control areas, the 10-cm zone, and the area beneath the carcass. At 10 cm from the carcass both the carrion and soil faunas were present but reduced (see Tables 1 and 2). Apparently the accumulation of decomposition products at this distance was sufficient to support some carrion feeders but insufficient to eliminate all of the soil dwellers. No carrion feeders were recovered from the control area.

IV. THE SOIL FAUNA

(a) The Effect of the Decomposing Carrion on the Soil and Vegetation

The decomposing bodies of the dead guinea pigs drastically modified the soil and vegetation in their immediate vicinity. Decomposition products passed into the soil during the black putrefaction and butyric fermentation stages. The excretory products of the various carrion-feeding insects, such as the ammonia produced by the large number of fly larvae (Mackerras and Freney 1933) and the acids associated with butyric fermentation, modified the chemical nature of the soil. The most obvious physical change in the soil was caused by hair and fluids which combine with plant litter to form a crust which remained considerably longer than a year. In addition, the soil structure was further modified by the burrowing activities of fly maggots and their predators before pupation.

By the time the carcass had decayed to the stage when only the bones remained, the area in its immediate vicinity showed marked differences in plant cover from the surroundings. The herbaceous vegetation beneath the carcass was killed, but a few inches away from it plants exhibited more vigorous growth (e.g. *Erharta longiflora* Sm. and *Briza maxima* L.) than in places further from the carrion.

(b) The Effect of the Decomposing Carrion on the Soil Fauna

Preliminary observations made a year prior to this study showed no differences between control samples and samples collected from beneath the carrion during the putrefaction stage of decomposition. Differences were evident, however, during the stage of black putrefaction.

Table 3 summarizes the differences between samples taken from beneath and at various distances from carrion. The effect of three stages of decomposition was readily observed for the various groups of arthropods. Table 4 gives the results of the statistical analysis of the differences in numbers of Collembola and Acari. They indicate a drastic reduction of these groups beneath the carcasses during the black putrefaction and butyric fermentation stages. Table 4 indicates that the decomposition products present in the soil during the black putrefaction or butyric

fermentation decomposition affected the soil fauna to a considerable depth beneath the carcasses, either reducing numbers or eliminating species.

From comparison of Tables 1, 2, and 3, and Figure 3, it is apparent that the soil animals normally engaged in the decomposition of plant litter and their predators had, in general, little or no tolerance for the concentrated decomposition products of carrion. Some decomposers were collected accidentally because of sampling inefficiency or interference by other animals like lizards and birds. The recovery of springtails (fam. Sminthuridae and Entomobryidae) from the zone beneath the carrion was the result of the sampling techniques, for it was impossible to prevent some of these from jumping into the sampling area when the carcass was removed. The complete absence of oribatid mites or subterranean springtails such as *Onychiurus* and *Tullbergia* spp. indicates, however, that the reduction of the typical soil fauna was very severe. It was greatest under the oral and anal parts of the carcass.

TABLE 3

DIFFERENCES IN THE NUMBERS OF COLLEMBOLA AND ACARI COLLECTED FROM BENEATH CARRION
AND AT VARIOUS DISTANCES FROM IT

Values are the geometric means—using the $\log(x+1)$ transformation—for 10 samples (area 43 sq. cm)

Stage	Groups	Control	Beneath Carrion	10 cm from Carrion	20 cm from Carrion
Black putrefaction	Collembola	56	15***	63	53
	Acari	556	82***	276***	576
Butyric fermentation	Collembola	64	4***	90	63
	Acari	693	58***	718	657
Dry decay	Collembola	136	85	114	101
	Acari	268	189*	251	317

* $P < 0.05$.

*** $P < 0.001$.

Of the scavengers, only earwigs (*Gonolabis woodwardi* Burr) and ants found the decomposing carcass attractive (see Fig. 3). The larger predators, e.g. centipedes and scorpions disappeared completely, whereas spiders aggregated and hunted on or around the carcass, particularly Lycosidae, Zodariidae, and Salticidae. No web-weaving spiders, e.g. *Plectochetus longissimus* Butler (Linyphiidae) were recovered from the samples collected from beneath the carcass during the butyric fermentation stage. One species of brachypterous bug (*Pirates*, fam. Reduviidae) was also often seen hunting around the carcass. The presence of other predators like staphylinid larvae in soil samples collected in the area immediately beneath the carcass could not be judged properly. These larvae were found regularly in control samples and it was difficult to distinguish them from those species of *Aleochara*, *Homalota*, and *Philonthus* which are associated exclusively with carrion.

The results of sampling at various distances from the carcass showed a zonation of arthropod communities. The most characteristic area was naturally the "carrion zone", that beneath the carcass. In this zone practically all the litter decomposers and their natural enemies were replaced by the carrion-frequenting arthropods. The "intermediate zone", i.e. the area surrounding the carrion to a distance of 10 cm contained a mixture of the two kinds of decomposer. The results suggest that some species tended to accumulate in this zone. Mobile litter dwellers, e.g. springtails (particularly *Entomobrya*, *Drepanura*, and *Katianna* spp.) and oribatid and bdellid mites, probably migrated into this zone from beneath the carcass. In the zone 10–20 cm from the carcass the soil fauna was virtually normal in composition. Samples showed no significant differences from those taken in the control area 40 cm from the carcass.

TABLE 4
NUMBERS OF COLLEMBOLA AND ACARI AT VARIOUS DEPTHS BENEATH AND AT 10 CM DISTANCE
FROM CARRION

Values are the means for four samples in the control zone, six samples beneath, and two samples 10 cm distant from carrion. Sample area 25 sq. cm

Soil Hor- izons	Soil Depth (cm)	Control	Collembola				Acari				
			Butyric Fer- mentation Stage		Dry Decay Stage		Control	Butyric Fer- mentation Stage		Dry Decay Stage	
			Beneath Carrion	10 cm from Carrion	Beneath Carrion	10 cm from Carrion		Beneath Carrion	10 cm from Carrion	Beneath Carrion	10 cm from Carrion
A0-A1	0-2	78.2	9.6	71.5	46.3	9.5	321.7	6.6	257.0	276.3	225.0
A1-A2	2-5	4.2	0.3	9.5	4.6	1.5	241.2	13.0	128.5	215.0	159.5
A2	5-9	2.2	—	4.5	3.0	0.5	86.0	29.6	52.0	149.6	93.0
A3-B	9-14	4.2	0.3	6.0	4.0	1.0	59.5	11.0	37.5	95.6	88.0

Redevelopment of the soil community beneath the carrion did not begin until after the heavy rains of June and July, 8 months after the carcasses were first put in the field. The first species to reappear were *Onychiurus* cf. *finetarius* L., *armatus* Tullb., and *Tullbergia* sp. (Collembola) and the numerous *Acerentulus westraliensis* Wom. (Protura). Mites were poorly represented by a few subterranean spp. of Oribatidae and Trombidiformes. One species of Pauropoda found an exceptionally favourable habitat in this zone as shown by their relatively high numbers in several samples.

Because of the encrustation of the surface litter its reinvasion was even slower than in soil horizons A1-3. Of the Collembola, *Folsomia* sp. was found frequently

in low numbers, while *Megalothorax swani* Wom. was exceptionally abundant in samples covered by algae. Mites were represented by several species in abnormally low numbers.

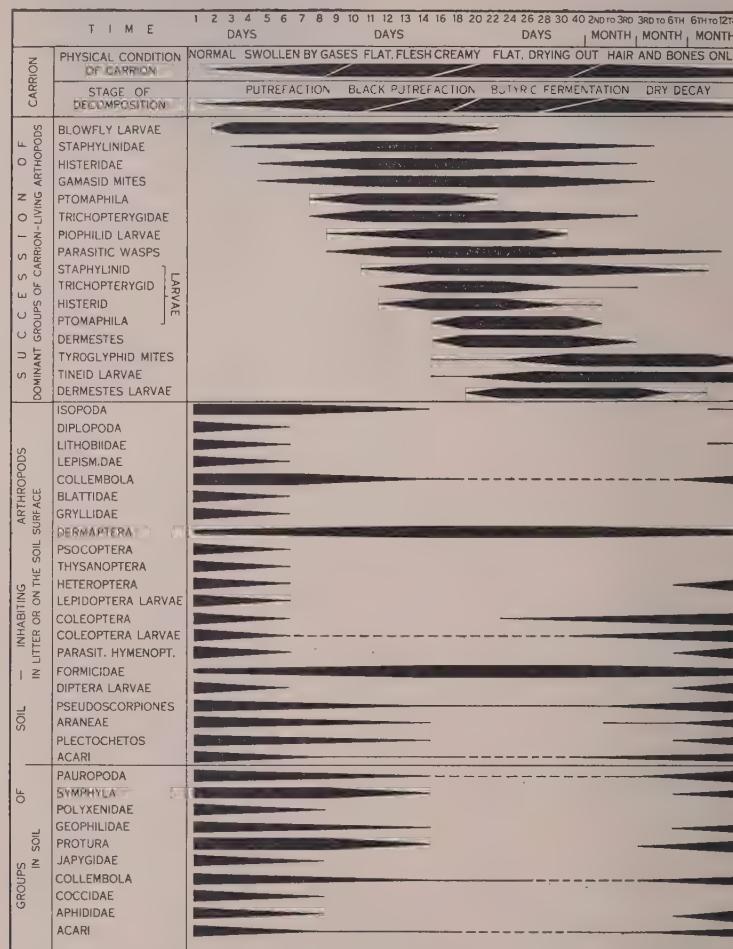


Fig. 3.—Diagrammatic summary of the results obtained. The almost complete disappearance of the soil dwellers while the carrion dwellers are most active is well marked. Variations in the thickness of each band indicate approximately the relative abundance within the groups at different times.

At the end of 12 months the carrion zone had not returned to normal (see Fig. 3) and many soil dwellers had not reappeared, suggesting that a much longer period would be necessary for complete redevelopment of the soil fauna.

V. DISCUSSION AND CONCLUSIONS

The succession of arthropods on decaying carrion has been described extensively by Megnin (1894), Dahl (1896), Tischler (1949), and Kühnelt (1950) for

European conditions. In general, their results are similar to those obtained in Australia by Fuller (1934, Canberra) and the present author (Perth).

Minor differences between results obtained by these workers and those of the present study are due either to zoogeographic, climatic, and edaphic factors or the methods employed. The larger silphid beetles, e.g. *Necrophorus* and *Pseudopelta* spp., play an important role at a characteristic stage in successions on decomposing carcasses in Europe (Megnin 1894, Kühnelt 1950). *Necrodes osculans* Vig. which occurs in tropical parts of Queensland and *Ptomaphila lachrymosa* which is common in temperate regions occur at what would be a comparable stage in this type of succession in Australian regions. In this investigation the presence of gamasid mites was characteristic of the black putrefaction and butyric fermentation stages. In contrast these mites were listed by Kühnelt as typical for the last stage of decomposition in successions on carrion in Europe. In addition, the gamasids were completely replaced by tyroglyphid mites during the dry decay stage, but these, however, were not mentioned by Kühnelt. Fuller's statement that mites were seldom seen during her investigation is attributable to her failure to sample the soil beneath the carcass. None of the other workers recorded relatively large number of trichopterygid beetles for, unlike the author, they did not use extraction methods for soil samples and traps. On the other hand, Trogidae, recorded by all other workers for the later stages of decomposition, were extremely rare in the King's Park samples. This is probably due to edaphic factors. As in Europe, *Trox* and *Megalotrox* spp. were commonly collected in dry carcasses found on the heavier soils adjacent to Perth. Also, in tropical parts of Western Australia, *Megalotrox* sp. preferred heavy soil types to sand, and further, this species regularly appeared on carcasses during earlier stages of decomposition.

Decomposition products which passed into the soil during various stages of decomposition adversely affected the soil, the plants present, and the associated fauna. No reference to this effect was found in the literature dealing with carrion. Fourman (1938), however, noted that under heavy accumulation of plant litter in wet places an increase in anaerobic bacterial activity resulted, when the various chemical products of decay, particularly phenols, not only killed the living plants but sterilized their seeds also. This destruction resembles that which occurred beneath the guinea pig carcasses. On the other hand, the vigorous plant growth around the carcasses indicates that the decomposition fluids were not so concentrated in this area, and that these had a stimulating effect on the herbage. The larvae of various carrion-dwelling insects which burrow into the soil for pupation and their contribution of organic substances to the soil by defecation etc. were probably responsible to some extent for the increased plant growth. This was the only contribution of the carrion-frequenting fauna to soil development observed during the investigation.

The study showed clearly that the soil fauna played only a minor part in decomposition of the carcasses. Ants and earwigs were the only members of the soil fauna observed to feed on the carrion. In addition, some soil-dwelling predators attacked carrion feeders and thus contributed to the decomposition. However, there is no doubt that the carrion created many unfavourable conditions for the vast majority of soil-dwelling arthropods and these unfavourable conditions persisted for more than 12 months.

VI. ACKNOWLEDGMENTS

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THE DISTRIBUTION OF THE EGGS OF MAMMALIAN LICE ON THEIR HOSTS

I. DESCRIPTION OF THE OVIPOSITION BEHAVIOUR

By M. D. MURRAY*

[Manuscript received September 3, 1956]

Summary

The behaviour patterns of *Damalinia ovis* (L.), *Linognathus stenopsis* (Burm.), and *Haematopinus eurysternus* Nitz. were found to be similar and readily divisible into three stages. In the first stage the louse sought the warm end of a temperature gradient. There it entered upon the second stage in which it remained stationary for a variable period with its head pointed towards the warm end. In *D. ovis* there was marked abdominal movement. The third stage lasted only 3 or 4 min and culminated in the deposition of the egg. In this stage the louse suddenly turned about and attached the egg to the fibre, sometimes backing into the warmer end first. This resulted in eggs being aligned similarly with the end of attachment nearest to the warm end of the temperature gradient.

It is suggested that the behaviour patterns of these lice are adapted to common physical characteristics of the environments in which they live, notably the presence of a temperature gradient.

I. INTRODUCTION

The lice of mammals fall into two orders, the Mallophaga, the biting lice, and the Anoplura, the sucking lice. Lice of both orders live in the hair coat of their respective hosts where they complete their whole life-cycle. The eggs may be laid on one part of the body of the host and not on another and are attached by a cement to a fibre of the coat, usually near to the skin with the end of attachment nearest to the skin. Some of the factors which determine these distributions will be described in this series of papers.

II. DAMALINIA OVIS (L.)

D. ovis, the biting louse of the sheep, is a mallophagan louse of the family Trichodectidae. Although much has been written on the control of this louse little is known of its biology. Scott (1952) studied the life-cycle both on the sheep and in the laboratory where she succeeded in rearing it for a few generations on a diet of skin scurf and yeast, at a constant temperature of 36.5°C. The complete life-cycle of *D. ovis* occupies about 34 days. There are five stages, namely, the egg, three nymphal stages, and the adult male and female. The nymphs and adults wander freely in the fleece but are commonly found near the skin where it is generally considered that they feed on epithelial debris. The eggs are always found near the skin.

This species was studied in detail because it was abundant and easy to handle and the behaviour of other species was compared with it.

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(a) The Microclimate of the Environment

Because of the density of wool fibres in the fleece, a blanket of still air is trapped around the body of the sheep. The skin on one side of this blanket of air and the atmosphere on the other are usually at different temperatures, so that a temperature gradient usually exists within the fleece.

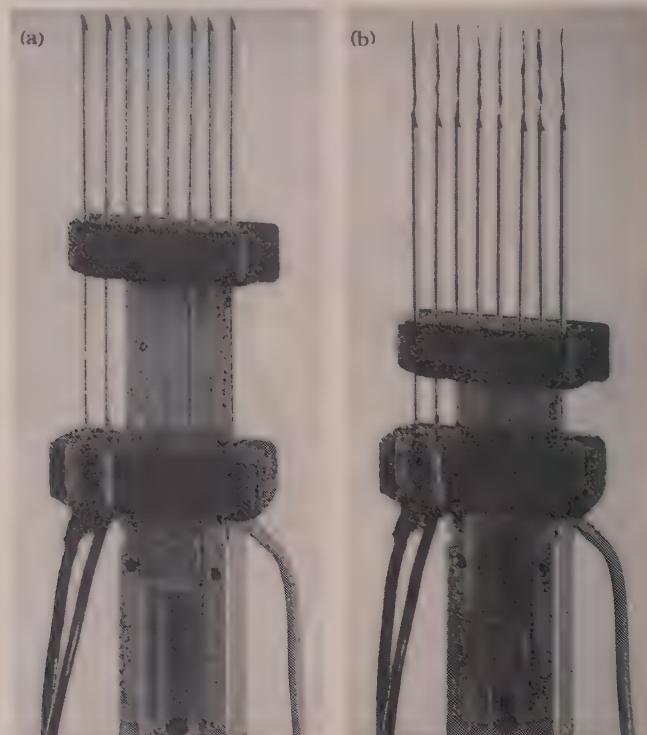


Fig. 1.—Arrangement of thermocouples in apparatus used to record temperatures in the fleeces of sheep. (a) Thermocouples ensheathed; (b) thermocouples exposed.

The temperatures in the fleece on the body of the sheep were measured with the apparatus shown in Figure 1. Basically it consisted of eight thermocouples in series made with fine constantan and copper wires to avoid the temperature being lowered by heat absorption and conduction. Each thermocouple was ensheathed in a hypodermic needle which could be withdrawn after insertion into the fleece. To measure temperatures, the fleece was quickly parted and the ensheathed thermocouples, held parallel to the skin, were thrust into the fleece at the desired depth. They were inserted for about $1\frac{1}{2}$ in. and the hypodermic needle sheath immediately withdrawn to prevent heat loss by conduction along it. Ten readings were taken on the galvanometer at 15-sec intervals, and the arithmetical mean was taken as the true temperature. This apparatus was not suitable for taking temperatures next to the skin, for which purpose individual fine thermocouples were used. The

temperature next to the skin was $37.5 \pm 1^{\circ}\text{C}$. A typical temperature gradient recorded in the fleece is shown in Figure 2. It will be observed that a sudden fall in the gradient occurred at the tip. This was because the fleece was more open at the tip and allowed some movement of air between the fibres. This fall in temperature at the tip was greater in fleeces shorter than 1 in., and less in the more gradual gradients encountered in fleeces longer than 1 in. Gradients of this type were recorded when the sheep were protected from the Sun.

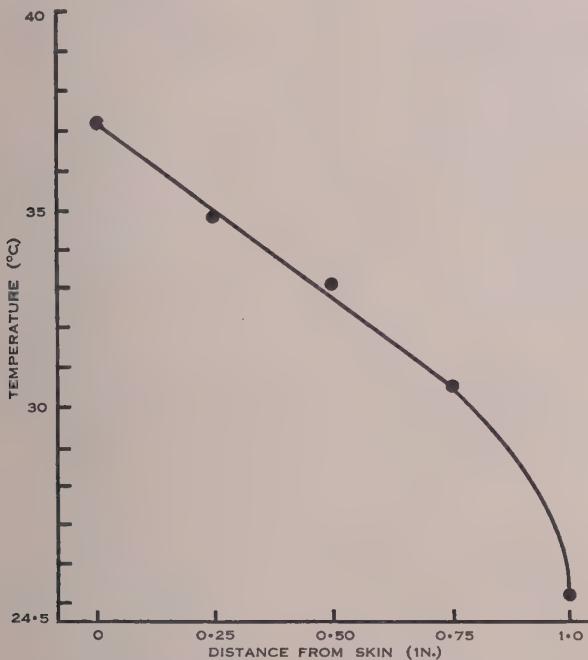


Fig. 2.—Temperature gradient in a 1-in. fleece when the atmospheric temperature was 24.5°C .

(b) Experimental

D. ovis were collected from heavily infested sheep with fleeces about 1 in. long. The area from which the lice were to be collected was covered with a white cloth and exposed to a source of warmth such as the Sun, an electric blanket, infra-red lamp, or an ordinary electric light bulb. The most convenient method was to place the sheep on a table and lower a 250-W infra-red lamp to within 3 ft of the cloth. In a few minutes the lice near the tip of the fleece migrated to the cloth, for which another was substituted every few minutes until the desired number of lice had been obtained. The lice were then collected from the cloths with a suction apparatus.

A temperature gradient from 43 to 19°C was produced in the laboratory by circulating water from two temperature sources through two well-insulated copper boxes. These boxes were kept 3 in. apart by a thin copper sheet which formed their

roofs. Along the copper sheet nine thermocouples were aligned $\frac{1}{4}$ in. apart. The thermocouple leads from the gradient were taken through a common switch to a spot galvanometer so that a series of readings could be made rapidly. The leads from the constant temperature source, supplied by water at the appropriate temperature in a "Thermos" flask, were taken direct to the galvanometer. Thermometers graduated in 0.1°C were used to determine the temperature of the water in the "Thermos" flasks. Temperature readings were taken across the gradient at intervals throughout the experiments, and between these intervals the reading of one thermocouple was observed frequently. The gradient was a straight line with a maximum fluctuation of $\pm 0.5^{\circ}\text{C}$.

The lice were placed on the copper sheet in a cell, the internal measurements of which were 2 by $\frac{3}{8}$ in. and 1 16 in. high. The floor of the cell was made of No. 1 Whatman filter paper which was marked with parallel pencil lines at $\frac{1}{4}$ -in. intervals along its length. The walls were made of cardboard and the roof was a clean glass slide. Wool from the sheep was spread evenly over the floor of the cell and, after the lice had been placed on it, the roof was sealed in position with cellulose tape. The cell was then placed on the copper sheet and, after the pencil lines had been aligned with the thermocouples, it was pressed firmly on to the copper sheet and fixed in position. Although the thermocouples were not within the cell it was established that the gradient within the cell became the same as that on the copper sheet within about 10 min. To observe the lice, vertical lighting was employed, and this did not appear to disturb them or influence their behaviour.

(c) Results

It was observed that about $\frac{1}{2}$ -1 hr before a louse was ready to lay an egg it moved to the warm end of the gradient and remained there until the egg was laid. During this period the louse invariably rested with its head in the direction of the warmest temperature. Also, during this period a considerable amount of contraction of the abdomen took place. At first the whole abdomen was contracted, first to one side and then to the other, or up and down, but these contractions gradually subsided until they were confined to the posterior tip of the abdomen. About 5 min before the egg was laid the louse suddenly turned round so that the posterior tip of the abdomen pointed in the direction of the warmest temperature. Some lice then "backed" towards the warmest regions of the gradient before commencing to lay the egg. First, the gonopods were raised away from the abdomen and by sweeping movements a fibre was "caught" and held next to the abdomen. After a few seconds the cement was excreted, then all the egg except the cap end was expelled. This appeared to be the result of an internal contraction because frequently the louse remained motionless throughout. After a short rest the louse completed oviposition by walking along the fibre and thus assisted in expelling the cap end of the egg. The actual act of egg laying took about 30 sec and after a short period the louse returned to the middle temperature of the gradient.

There was a tendency for ovipositing lice to come to rest near to another ovipositing louse or egg.

III. OBSERVATIONS ON OTHER SPECIES OF LICE

(a) *Linognathus stenopsis* (*Burm.*)

This is a sucking louse (Anoplura) from the goat. The same type of cell was used in which hair from the goat was aligned longitudinally, and the same temperature gradient was established within the cell. When fully engorged this louse will lay eggs under laboratory conditions at the rate of two a day for 2 days before requiring another blood meal. Consequently each louse laid at least two eggs in this experiment and all were laid at the warm end of the gradient. The oviposition behaviour was similar to that of *D. ovis*. The louse left the middle temperature zone and moved to the warm end where it remained for several minutes, its head towards the warm end. Suddenly it turned about and grasped the fibres with its gonopods. The louse paused and the milky white cement was excreted onto the fibre, surrounding it between the gonopods which acted as a mould. After about 15 sec. by which time the surface of the cement was seen to dry, the abdomen was arched, the gonopods removed from the fibre, and the egg expelled as the louse walked along. The louse paused for about $\frac{1}{2}$ min after laying the egg and contracted its abdomen longitudinally. After relaxing the abdomen, it returned to the 32°C zone of the gradient.

(b) *Haematopinus eurysternus* (*Nitz.*)

This is a sucking louse from cattle and unlike *L. stenopsis* it does not engorge with blood to the same extent but has smaller blood meals more frequently.

The same type of cell, with cattle hair, and the same temperature gradient was used. The lice were again distributed mainly in the 32°C zone. Two lice were observed to oviposit. To lay an egg, they moved to the warm end and rested with their heads pointed to the warm end for a few minutes. They then turned about, held the fibre in a groove formed by the gonopods next to the abdomen, and backed into the warmest temperatures of the gradient. There the abdomen was rubbed up and down the fibre, which was held between the claspers. After a short pause the cement substance was excreted rapidly, covering the fibre, and filling the gap between the fibre and the gonopods which acted as a mould. About 10 sec later, when the cement showed surface hardening, it was pulled out to form a stalk, after which the abdomen was arched and the egg expelled as the louse walked along the fibre to return to the cooler temperatures.

(c) *Boopia* sp.

This mallophagan louse was obtained from the long-nosed bandicoot, *Potorous nasuta* Geoffroy, a small marsupial common in the environs of Sydney. The lice were placed on a temperature gradient of from 40 to 30°C with hair from the bandicoot. Eggs were laid at the warm end of the gradient and the end of attachment in each case was towards the warm end.

IV. DISCUSSION

At the time of egg laying the lice entered upon a definite behaviour pattern which could be divided into three stages. In the first the louse moved to the warm

end of the temperature gradient where it remained until the egg was laid. The main visible features of the second stage with *D. ovis* were the pointing of the head towards the warm end and the abdominal movements. In *L. stenopsis* and *H. eurysternus* the head was also pointed towards the warm end but abdominal movements were not observed. The duration of this stage varied but was longest for *D. ovis* and shortest for *H. eurysternus*. In the third stage the louse turned about, grasped a fibre, and an egg was laid. Although there were differences between the species at this stage, in each case a stimulus was produced which caused the secretion and excretion of the cement. It has been stated in the literature (Buxton 1947) that the cement is excreted at the same moment as the egg is laid. In the species studied and in *Pediculus humanus* L., head louse, (Murray, unpublished data) the cement was excreted suddenly and the egg was not expelled until some 15 sec later when the surface of the cement showed some hardening. Variations in the shape of the cement attachment appeared to be related to the use of gonopods. If the gonopods were not used as a mould for the cement, relatively untidy attachment resulted as with *D. ovis*. When the gonopods were used as a mould, the attachment was tidy as with *L. stenopsis* and *H. eurysternus*. The shape and manner of use of the gonopods as moulds for the cement undoubtedly leads to attachments which may be characteristic for a species.

In the species studied there were marked similarities in the oviposition behaviour and it seems likely that the behaviour, at the time of oviposition, of other species of mammalian lice is similar. The distribution of the eggs in the cells used in the laboratory was similar to that found naturally in the coats of their respective hosts. This suggests that the behaviour patterns of these lice are adapted to the common physical characteristics of the environments in which they live, notably to the presence of a temperature gradient.

V. ACKNOWLEDGMENT

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THE DISTRIBUTION OF THE EGGS OF MAMMALIAN LICE ON THEIR HOSTS

II. ANALYSIS OF THE OVIPOSITION BEHAVIOUR OF *DAMALINIA OVIS* (L.)

By M. D. MURRAY*

[Manuscript received September 3, 1956]

Summary

The behaviour pattern of *Damalinia ovis* (L.) is adapted to the physical features of the environment in which the louse lives.

In stage 1, the louse was attracted to temperatures between 35 and 40°C and this temperature zone was necessary for oviposition to proceed satisfactorily. Optimum temperature conditions were between 37 and 39°C. In stage 2, the louse orientated itself so that its head was directed towards the warm end of a temperature gradient or towards the saturated end of a humidity gradient, but when these gradients were antagonistic the orientation to temperature dominated. At the commencement of stage 3, the louse reversed its orientation to both temperature and humidity gradients but again the attraction to temperature was dominant. Before egg laying commenced, a fibre of suitable diameter had to be caught by a gonopod and held next to the abdomen. The resulting tactile stimulus was critical and its absence inhibited oviposition. Other factors which influenced oviposition were the depressant effect of high humidities, the orientation to light, and the attraction to other ovipositing lice and eggs.

I. INTRODUCTION

The oviposition behaviour of some mammalian lice and the division of the behaviour pattern into three stages has been described in Part I of this series (Murray 1957). It was found that when female *Damalinia ovis* (L.), *Linognathus stenopsis* (Burm.), *Haematopinus eurysternus* (Nitz.), and a *Boopia* sp. were placed, together with wool or hair from their host, in a temperature gradient which simulated that found in the host's hair coat, the distribution of the eggs laid was similar to that found naturally. This suggested that the behaviour patterns were adapted to the common physical characteristics of the environments of the lice. In these experiments, external stimuli which might influence the oviposition behaviour could have originated from the fibres, from variations in temperature, humidity, and light, or from the presence of other lice.

This paper presents the results of a study of the influence of these factors on the oviposition behaviour of *D. ovis*.

II. THE INFLUENCE OF THE FIBRE

(a) *The Nature of the Fibre*

It was found that *D. ovis* would attach eggs readily to glass wool or 1½-denier "Nylon". To determine whether these materials were suitable for oviposition

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experiments, two collections, each of approximately 1500 lice,* were divided into three groups. One group was placed in a glass tube with glass wool, another with wool which had been scoured with ether and water to remove all traces of sweat and sebaceous gland secretions, and the third with natural wool from the sheep. The wool and the lice were removed from the same sheep. All groups were exposed to 37.5°C and the humidity was maintained at 60 per cent. R.H. by means of sulphuric acid solutions (Solomon 1951). The number of eggs was counted after 36 hr

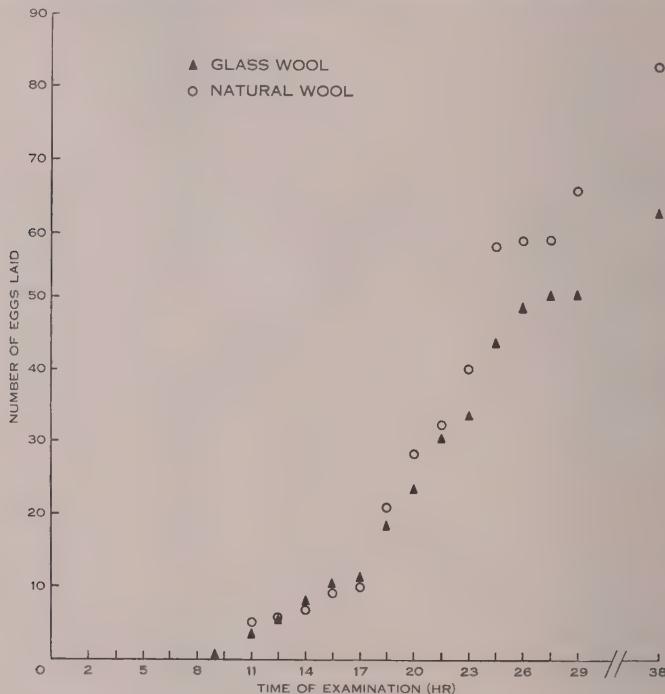


Fig. 1.—Comparison of rate of oviposition of *D. ovis* on glass wool and on wool from sheep when exposed to 37.5°C.

and again after 60 hr. In the tubes containing scoured wool 13 per cent. of the lice laid eggs and 23 per cent. of the lice laid eggs in each of the other tubes. However, after another 24 hr, 37 per cent. of the lice on natural wool had laid eggs whereas no more eggs had been laid on the scoured wool or on glass wool. It was observed that after this period the majority of the lice on scoured and glass wool were dead.

In a further experiment, about 600 lice were randomly divided into six groups. Three of these groups were placed in cells with wool of the same sheep from which they were collected and the other three groups were placed in cells with glass wool. All groups were exposed to 37.5°C and examined at $1\frac{1}{2}$ -hr intervals. As may be seen in Figure 1, no eggs were laid for the first 9 hr. For the next 12 hr eggs were laid at a similar rate in each group, but for the remaining 17 hr more eggs were laid in the cells containing natural wool. Over this period there was again a greater

* Throughout this paper the term "lice" will refer to female lice.

mortality of lice in the cells containing glass wool. After 29 hr, 24 per cent. of the lice on glass wool were dead and on the natural wool 20 per cent. were dead. This mortality had risen to 56 per cent. on glass wool and 36 per cent. on natural wool, when the experiment concluded 9 hr later.

(b) *The Presence of a Fibre*

Two collections of lice were each divided into two groups. One group was placed in a glass tube with no fibre material and the other group in a similar tube with glass wool. Both groups were exposed to 37.5°C and the relative humidity was maintained at 60 per cent. After 36 hr, the number of eggs laid was counted. In the first experiment, 380 lice were placed in the tube without glass wool and one egg was laid whereas 62 eggs were obtained from 381 lice in the tube with glass wool. In the second experiment, three eggs were laid by 506 lice in the tube without glass wool and 161 eggs by 589 lice in the tube with glass wool. Examination of the lice in the tubes without fibres revealed that the egg within many of the lice had developed to maturity (see Section III(b)). A population of lice which contained a high percentage of females ready to oviposit was frequently required in subsequent experiments and was obtained by withholding fibres from the lice for 24 hr prior to the experiment.

(i) *Influence on Stage 2 of the Behaviour Pattern.*—Lice were placed in four cells along which a temperature gradient from 20 to 40°C was established. In cell 1, there were no fibres present; in cell 2, glass wool fibres were placed so that a louse could move freely on one fibre along the gradient but at no time was it possible for its abdomen to come into contact with any other fibre; in cell 3, the number of glass wool fibres was such that the abdomen of the louse was at all times in contact with several fibres; and in cell 4, no fibres were present but the roof of the cell was lowered so that the abdomen of the louse was at all times in contact with it and the floor. In all cells the lice moved to the warm end and the only difference observed in stage 2 was that the abdominal movements of the lice in cells 1 and 2 were not as vigorous as those of the lice in cells 3 and 4. Only the lice in cells 2 and 3 laid eggs and there was no difference in the duration of stage 2 between the lice in these two cells. When glass wool was added to cells 1 and 2 so as to make the density of the fibres in these cells similar to that in cell 3, vigorous abdominal movement commenced immediately.

(ii) *Influence on Stage 3 of the Behaviour Pattern.*—Another collection of lice was divided into three groups. They were placed in similar glass tubes and exposed to 37.5°C and a relative humidity of 60 per cent. In one tube was placed glass wool, the fibres of which were approximately 0.02 mm in diameter, in another, glass fibres approximately 0.1 mm in diameter, and in the other, glass fibres ranging from 0.2 to 0.35 mm. On 0.02-mm glass wool 200 lice laid 22 eggs, on the medium-sized fibres 255 lice laid two eggs, and 407 lice on the widest fibres laid four eggs. Similar results were obtained on repetition. It was observed that the louse was unable to hold the larger fibres between the gonopod and abdomen.

Thus the presence of a fibre which could be held next to the abdomen by a gonopod was necessary for egg laying to take place.

III. THE INFLUENCE OF TEMPERATURE

(a) On the Number of Eggs Laid

Five collections, each of 8000–10,000 lice, were made and all the lice of each collection were exposed to one of the following temperatures: 32·5, 35, 37·5, 40, or 42°C. Another collection of 20,000 lice was divided into four groups and each group was exposed to either 32·5, 35, 37·5, or 40°C. The relative humidity was maintained at 65 per cent. and the number of eggs laid was counted after 48 hr.

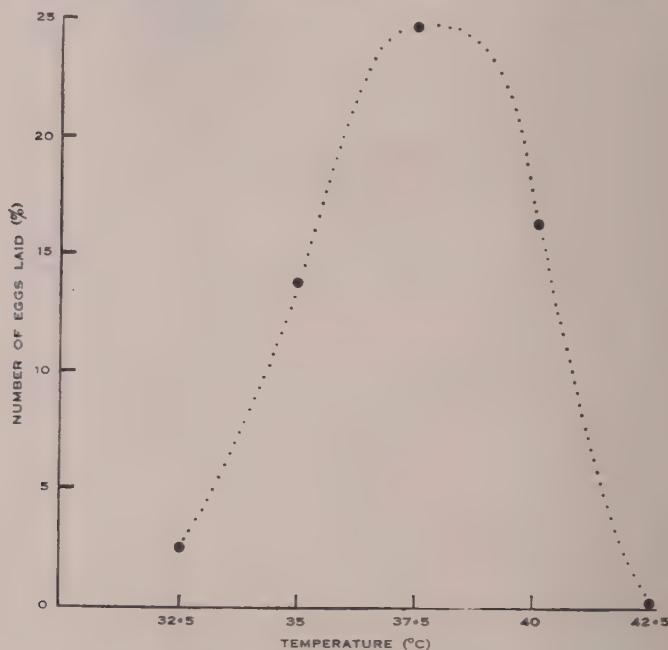


Fig. 2.—Influence of temperature on the number of eggs laid by *D. ovis*.

The results are shown in Figure 2 from which it will be seen that temperature had a profound influence on the number of eggs laid. The number of eggs laid increased as the temperature rose from 32·5 to 37·5°C and there was a decline in the number laid at 40°C. At 42°C no eggs were laid and all the lice died within 18 hr.

A further collection of lice was divided into five groups and each group was exposed to 42°C at either 20, 40, 60, 80, or 100 per cent. R.H. Again all the lice died within 18 hr without an egg being laid.

The failure to lay eggs at 42°C was, therefore, due to the lethal effect of this temperature. The variation in the number of eggs laid in the other groups may have been due to an effect of the temperature on the development of the egg within the louse or to an effect on the act of oviposition.

(b) On the Development of the Egg within the Female

Only one egg develops at a time in *D. ovis*. Its length can be measured by placing the louse between two glass slides and examining the abdomen under the

microscope. The weight of a slide does not injure the louse but flattens the abdomen sufficiently to enable the egg to be seen when light is transmitted through the abdomen. The earliest stage which can be detected measures 0.2 mm and a fully developed egg 0.85 mm.

The length of the developing egg within 163 lice was measured. The lice were then divided into four groups, the first contained 34 lice in which no developing egg was visible; the second, 62 lice with an egg 0.2–0.48 mm in length; the third, 44 lice with an egg 0.49–0.72 mm in length; and the fourth, 23 lice with an egg longer than 0.72 mm. All lice were kept on glass wool at 37.5°C until egg laying

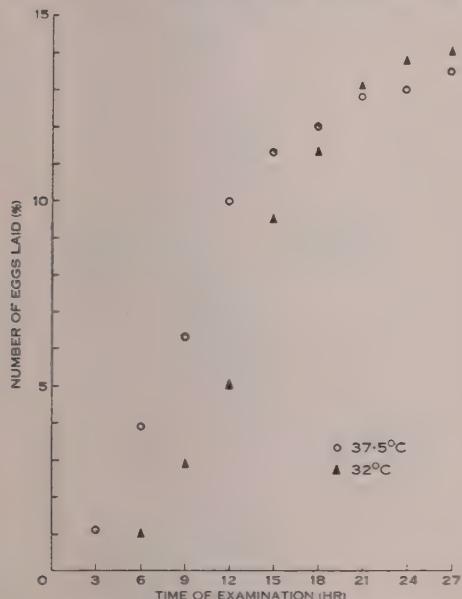


Fig. 3.

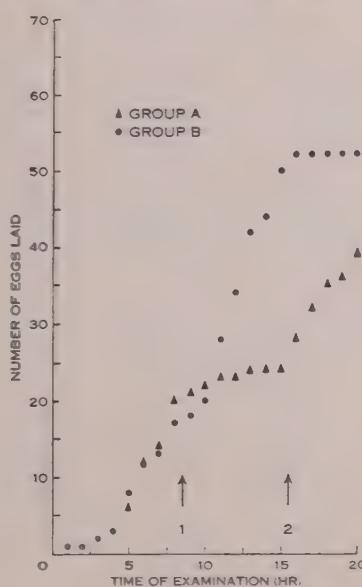


Fig. 4.

Fig. 3.—Influence of temperature on the development of the egg within *D. oris*. Both groups prevented from ovipositing for 24 hr by withholding fibres during which time group O kept at 37.5°C and group ▲ kept at 32°C. Both groups then presented with fibres and exposed to 37.5°C.

Fig. 4.—Influence of temperature on oviposition by *D. oris*. Both groups exposed initially to 37.5°C. At 1, group A exposed to 32°C whilst group B was kept at 37.5°C. At 2, group A returned to 37.5°C and group B exposed to 32°C.

had ceased. No eggs were laid in the first two groups. 28 eggs were laid in the third group, and 10 in the fourth. From these results it may be concluded that when lice are starved, as in these experiments, only those which contain an egg longer than 0.48 mm when collected subsequently lay an egg.

From another collection were obtained 52 lice, each containing an egg 0.46–0.72 mm in length. These lice were randomly divided into group A, the mean egg length of which was 0.57 mm, and group B, with a mean egg length of 0.58 mm. Fibres were not provided for either group. Group A was exposed to 37.5°C and group B to 32°C at 60 per cent. R.H. The egg lengths were measured after 24 hr when the mean

egg length of group A had increased to 0.80 mm and that of group B to 0.78 mm. Thus the lower temperature did not materially affect the development of the egg.

A further collection of about 1000 lice was divided into two groups. One group was exposed to 37.5°C without fibres and the other to 32°C, also without fibres. After 24 hr each group was given glass wool and placed at 37.5°C. Examinations were made every 3 hr and the number of eggs laid was recorded. The results are presented in Figure 3 from which it is apparent that exposure to 32°C delayed egg laying slightly.

(c) *On Oviposition*

Another collection of 800 lice was kept at 37.5°C for 30 hr without fibres and was then divided into five groups. Each group was given glass wool and exposed to either 32.5, 35, 37.5, 40, or 42°C for 12 hr after which the eggs laid were counted. The experiment was repeated with another 600 lice and the results were combined. At 32.5°C 3.7 per cent. of the lice laid eggs; at 35°C, 14.7 per cent.; at 37.5°C, 26 per cent.; at 40°C, 21 per cent.; and at 42°C, 5.5 per cent. laid eggs.

From another collection, 240 lice with a developing egg of 0.72 mm or over were selected. These were randomly divided into two groups, A and B. After a period of 24 hr at 37.5°C without fibres, glass wool was inserted. Both groups were still exposed to 37.5°C and examinations were made hourly to count the number of eggs laid. When oviposition had been in progress 8 hr, group A was transferred to 32°C while group B was kept at 37.5°C. After another 8 hr group B was transferred to 32°C and group A returned to 37.5°C. The results are shown in Figure 4 from which it may be seen that the rate of egg laying decreased as soon as the lice were exposed to 32°C and was restored when they were returned to 37.5°C. Similar results were obtained when the experiment was repeated.

(d) *On the Distribution and Alignment of the Eggs*

Lice were placed in cells with glass wool and exposed to a constant temperature of 37.5°C. Others were placed in similar cells with glass wool and exposed to temperature gradients of either 32–40°C, 19–43°C, 19–47°C, or 12–56°C. As may be seen in Figure 5(a), the eggs of the lice exposed to the constant temperature were randomly distributed on the fibres in the cell whereas those on the temperature gradients were laid in the zone 35 to 42°C (Figs. 5(b)–5(e)). In addition, of 254 eggs laid in the cells exposed to the constant temperature, 126 were aligned in one direction and 128 in the other, whereas in each of the gradients, over 78 per cent. of the eggs were aligned with the end of attachment towards the warm end.

(e) *On the Behaviour Pattern*

Lice were placed on a temperature gradient of 20–40°C. Those preparing to oviposit moved to the warm end but were prevented from proceeding beyond the 30°C zone. They remained there with their heads towards the warm end but there was no abdominal movement. After 5 hr, they were allowed to move to the 40°C zone and normal abdominal movements soon commenced. No eggs were laid during the first hour in the 40°C zone.

Other lice were exposed to a temperature gradient, the warm end of which was 37°C. When three lice had commenced stage 2 and two lice had commenced stage 3, the temperature at the warm end was dropped from 37°C to 26°C. Eggs were not laid until the temperature had been restored to 37°C. 3 hr later. The lice which had commenced stage 2 laid their eggs within a $\frac{1}{2}$ -1 hr and those which had commenced stage 3 within 5 min.

Further lice were exposed to a gradient of 34–40°C distributed over 1 in. and when two had commenced stage 2 the gradient was reversed. The lice turned about and moved to the warm end. The gradient was reversed again and once more the lice turned about and moved to the warm end.

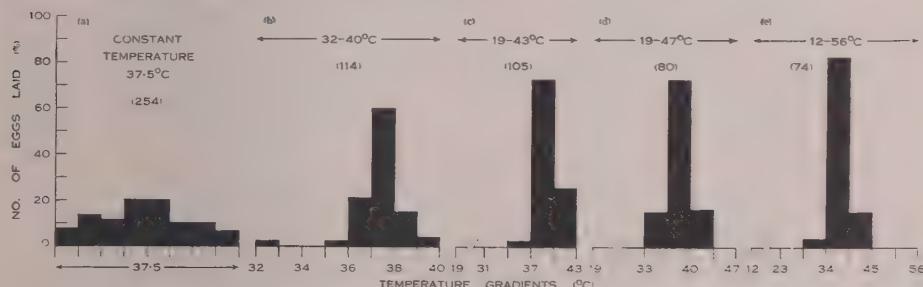


Fig. 5.—(a)–(e) Distribution of eggs of *D. ovis* on various temperature gradients. Number of eggs laid on each temperature gradient shown in parenthesis on the figure.

IV. INFLUENCE OF HUMIDITY

(a) On the Number of Eggs Laid

Three groups of lice on glass wool were exposed to relative humidities of 95, 60, or 20 per cent., and kept at 37.5°C. After 48 hr. the number of eggs laid was counted. The experiment was repeated twice. The results are presented in Table I, from which it may be seen that, although there was a difference in the number of eggs laid by each collection, in each, more eggs were laid at 60 or 20 per cent. R.H. than at 95 per cent. R.H. Using the χ^2 test these results were shown to be significant. There were also significantly more eggs laid at 60 than at 20 per cent. R.H.

(b) On the Distribution of the Eggs

The circular, humidity-choice chambers used were basically similar to those used by Wigglesworth (1941). The arena in which the lice were placed was 1 mm in height and its floor was made of organdie. Humidity was controlled with saturated salt solutions and measured with cobalt thiocyanate papers (Solomon 1945). In all experiments the lice within the chambers were exposed to 37.5°C for 48 hr. In 16 experiments the air in one-half of the arena was kept over calcium chloride and was almost dry and the air in the other half was kept over wet sand and was nearly saturated. A total of 187 eggs was attached to the frayed fibres of the organdie in the almost dry atmosphere and 17 in the nearly saturated atmosphere.

Other lice were placed either in experimental chambers in which the relative humidity was 33 per cent. in one-half and 75 per cent. in the other, or in control

chambers in which the relative humidity was 75 per cent. throughout. Glass wool was spread evenly over the organdie floor of the arenas of the chambers. In the three control chambers a total of 93 eggs was laid, 51 in one half and 42 in the other half, whereas in the six experimental chambers a total of 212 eggs was laid, 148 in the 33 per cent. R.H. atmosphere and 64 in that of 75 per cent. R.H.

TABLE I
INFLUENCE OF HUMIDITY ON THE NUMBER OF EGGS LAID BY *D. OVIS*

Collection	95% R.H.		60% R.H.		20% R.H.	
	No. of Lice	No. of Eggs (%)	No. of Lice	No. of Eggs (%)	No. of Lice	No. of Eggs (%)
A	700	17.3	481	25.6	590	21.2
B	587	11.2	573	25.5	882	26.6
C	656	3.8	400	7.5	934	6.4
Total	1943	10.9	1454	20.6	2406	17.5

Humidity-choice chambers were then constructed on a copper sheet along which a temperature gradient was established so that one-half of the arena was in the temperature zone of 20–30°C and the other half in the zone 30–40°C. In one-half of the arena the air was saturated with water vapour, in the other half the air was dry. In each experiment, two chambers were used and the humidities were reversed. Thus, in one the saturated atmosphere and in the other the dry atmosphere was at the warm end of the gradient. The oviposition behaviour was normal under both experimental conditions. Eggs were laid only at the warm end and all of the 110 eggs laid were aligned with end of attachment towards the warm end. The distribution of the eggs was determined by temperature preference and not by humidity preference.

(c) On the Alignment of the Eggs

The dividing partitions of the humidity-choice chambers were increased from 1 to 8 mm in width so as to increase the length of the humidity gradient in this region. Parallel "Nylon" fibres were attached to the floor in this region so as to lie along the gradient. In the experimental chambers, calcium chloride was placed in one half and sand saturated with water in the other. The relative humidity within the control chambers was 33 per cent. The lice within the chambers were exposed to 37.5°C for 48 hr. In the four control chambers, 136 eggs were laid and the end of attachment of 67 was in one direction and that of 69 in the other. A total of 205 eggs was laid in 16 experimental chambers and 187 of these were aligned with the end of attachment towards the saturated end. The results as depicted by these totals were consistent in all chambers.

A louse preparing to lay an egg rested with its head towards the saturated end of the gradient but shortly before the egg was laid it turned about so that its head was towards the dry end of the gradient.

In another cell, along which there was a temperature gradient of 20–40°C, a humidity gradient was established so that the humidity was low at 40°C and high at 35°C. "Nylon" fibres, which ran parallel to the gradients, and a small strip of cobalt thiocyanate paper to demonstrate the presence of the gradient, were placed in this region of the cell. Lice were kept at 37.5°C without a fibre for 24 hr before they were placed in the cell. In the first experiment, 15 eggs were attached to the fibres with the attachment towards the warm end and eight with the attachment towards the cool end; in the second experiment, the end of attachment of 40 of the 45 eggs laid was towards the warm end; and in the third 34 of the 48 eggs laid were attached in this manner. The lice orientated themselves to the temperature gradient rather than to the humidity gradient.

V. INFLUENCE OF LIGHT

Lice were placed in cells each of which had one half shaded and the other half exposed to daylight. The temperature within the cells was kept at 37.5°C. Of the 168 eggs laid, 122 were laid in the shaded areas.

Along similar cells was established a temperature gradient of 20–50°C so that the temperature zone 20–30°C was shaded and the zone 30–50°C exposed to strong daylight directed along the gradient from the warm end. The oviposition behaviour was uninfluenced and, of the 36 eggs laid in this experiment, 33 were laid in the temperature zone 41–35°C in the lighted area and the ends of attachment were towards the warm end of the gradient.

VI. INFLUENCE OF THE PRESENCE OF OTHER LICE AND EGGS

Lice kept singly in cells on a temperature gradient of 20–40°C behaved normally and laid their eggs at the warm end with the end of attachment towards the warm end. When other lice were present it was observed that lice in stage 2 frequently congregated in groups before any eggs had been laid. When some eggs had been laid there was a tendency for others to be laid next to them.

VII. DISCUSSION

In the initial experiments it was shown that *D. ovis* would attach eggs readily to synthetic fibres. There was no difference between the time of commencement or the rate of oviposition between two groups of lice one of which was offered glass wool and the other wool from the sheep, so the influence of the fibres was associated with their physical rather than with their chemical characteristics.

(a) Stage 1

Lice were exposed to a constant temperature and humidity and eggs were randomly distributed on the fibres within the cell. When a choice was given between

air that was nearly saturated with water vapour and air that contained hardly any water vapour, or between air at 75 per cent. R.H. and air at 33 per cent. R.H., most eggs were laid in the drier atmosphere. However, eggs were laid at the warm end of a temperature gradient of 20–40°C. regardless of the prevailing humidity. Strong daylight, directed along the gradient from the warm end, did not influence this movement towards the warm end. In stage 1, therefore, the lice were attracted to warmth and in particular to temperatures between 35 and 40°C.

(b) Stage 2

Orientation to any particular direction was not seen when lice were exposed to constant temperature and humidity. However, orientation was apparent when they were exposed to either a temperature gradient without a humidity gradient or to a humidity gradient without a temperature gradient. In the presence of antagonistic temperature and humidity gradients, the orientation to temperature dominated. When lice were in stage 2, and the gradient was reversed, they turned about to rest again with their heads towards the warm end. Orientation to temperature also dominated the normal negative phototactic behaviour.

Exposure of lice to different constant temperatures influenced greatly the number of eggs laid and it was shown that at temperatures lower than 42°C, which was lethal, the effect was exerted at the time of oviposition. It may also be seen from Figure 4, that when lice were held at 32°C and were then restored to 37.5°C, the rate of oviposition was similar to that of lice kept at 37.5°C throughout. If stage 3 only had been affected all the eggs would have been laid within $\frac{1}{2}$ hr because only 5 min are required for stage 3 to be completed. When lice were placed on a gradient which only permitted them to reach a temperature of 30°C, no egg was laid until they were subsequently kept for 1 hr at 35–40°C. Again, when lice were in stage 2 and the temperature was dropped from 37.5 to 26°C, no eggs were laid until the temperature was restored to 37.5°C. Temperature, therefore, influenced stage 2.

Humidity influenced the number of eggs laid but only high humidities had a severe effect and in all experiments concerning temperature the relative humidity was kept at 60 per cent. or lower. Clearly, temperature was a critical factor and influenced, in all probability, the systems controlling the passage of the egg down the genital tract.

It is reasonable to assume that abdominal movements were associated with the passage of the egg as they ceased at temperatures of 30°C and lower. Fibre density influenced the vigour of abdominal movements. They were less obvious when fibres were sparse, but there was no evidence that stage 2 was prolonged as a consequence. When lice were placed in cells in which the roof was lowered so that the abdomen was always in contact with the floor and roof of the cell, the abdominal movements were of the usual vigorous type. It would appear, therefore, that the number of tactile stimuli received by the abdomen determined the vigour of the abdominal movements.

During this stage, lice were attracted to other ovipositing lice.

(c) Stage 3

For the satisfactory completion of stage 3, it was again necessary for temperatures to be in the region of 37.5°C. When lice were exposed to a constant temperature and humidity, eggs were aligned along the fibre in either direction. In a temperature gradient without a humidity gradient, eggs were aligned with the end of attachment towards the warm end, and in a humidity gradient without a temperature gradient, eggs were aligned towards the high humidity. However, in the presence of antagonistic temperature and humidity gradients, the orientation to temperature dominated.

Before egg laying commenced, one of the gonopods was raised from the abdomen and a fibre held between it and the abdomen. When a fibre was not present or the fibre was too great in diameter to be held egg laying was inhibited. A tactile stimulus was required before egg laying could proceed. This stimulus is probably similar to that required by the silkworm moth, *Bombyx mori* (L.), in which it has been shown to operate as a simple reflex through the posterior abdominal ganglion (McCracken 1907).

In the oviposition behaviour there were two distinct phases. In the first, stage 1 of the behaviour pattern, the louse sought a temperature zone in which oviposition could proceed. The second phase, stages 2 and 3, was concerned with the passage of the egg down the genital tract and its deposition. The two critical requirements during this phase were correct temperature conditions and the presence of a fibre of suitable diameter. These requirements being satisfied, other factors, such as orientation to temperature and humidity, orientation to light, attraction to other ovipositing lice and eggs, and the effect of high humidities, exerted their influences.

It will be apparent that these factors can influence both the distribution and the abundance of the eggs of *D. ovis*, but the ecological implications arising from the manner in which they vary in the natural environment will be discussed in a subsequent paper.

VIII. ACKNOWLEDGMENT

I wish to thank Dr. D. F. Stewart, Officer-in-Charge, McMaster Laboratory, for his many helpful suggestions during the preparation of this paper.

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STUDIES IN AUSTRALIAN AMPHIBIA

I. THE GENUS CRINIA TSCHUDI IN SOUTH-WESTERN AUSTRALIA AND SOME SPECIES FROM SOUTH-EASTERN AUSTRALIA*

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Summary

The Western Australian representatives of the genus *Crinia* Tschudi are reviewed. On the basis of field observations and data from *in vitro* crosses it is concluded that the following species occur in south-western Australia: *Crinia rosea* Harrison, *C. leai* Fletcher, *C. georgiana* Tschudi, *C. glauerti* Loveridge, *C. insignifera* Moore, and a new species. From *in vitro* crosses, Moore's (1954) conclusion that *C. signifera* Girard does not occur in the south-west of Australia is confirmed. *C. glauerti* is regarded as a western representative of the *C. signifera* super-species.

Collections in eastern Australia revealed the presence of an undescribed species which is a representative of the *C. insignifera* super-species.

Life history data are presented.

I. INTRODUCTION

The genus *Crinia* Tschudi was last reviewed by Parker (1940) who recognized five species from Western Australia as follows: *Crinia rosea* Harrison, *C. leai* Fletcher, *C. georgiana* Tschudi, *C. signifera* Girard, and *C. glauerti* Loveridge. Finch (1951) has shown that, in *Crinia*, morphological structures frequently used in the past to establish species are unreliable, but agreed with Parker that these were five valid species. The work of Finch indicated the advisability of using reproductive isolation in order to check the status of species erected on morphological features alone (this type of work was commenced by the present author in 1952).

The usual difficulties of amphibian taxonomy have been accentuated in the present work because some specimens respond differently to preservation in alcohol or formalin and many valid species lack morphological distinctness or such differences are minute. Moore (1954) has shown that specimens of *C. signifera* from eastern Australia when crossed with morphologically similar animals from Western Australia produced inviable embryos, indicating that the western population was a valid species for which the name *C. insignifera* Moore was proposed. The present enquiry developed by analysing male calls and completing hybridization experiments. After species had been determined on biological evidence they were named according to the morphological species described in the literature. In cases where this was not possible the presence of sibling species was indicated. The results are grouped in the following order: those species where adequate morphological differences exist, those sibling species suggested on differences of male call, and finally the hybridization experiments in which the two preceding categories of species were tested for inviability.

* Part of a thesis submitted for the degree of Doctor of Philosophy in the University of Western Australia.

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II. MATERIALS AND METHODS

Animals used in hybridization experiments were taken from breeding congresses when calling males and females with uterine eggs were present. Gravid females were used the day following capture. *C. signifera* was collected in New South Wales (Port Hacking by Mr. W. B. Malcolm and East Lindfield by Dr. Barbara Y. Main) and flown to Perth where gravid females still retained uterine eggs.

Males were sometimes successfully held for periods of 3 or 4 weeks by keeping them in a room at 16°C and washing them in tap-water each day. All crosses were made in conditioned tap-water (Rugh 1948, p. 10) in a constant temperature room at 16°C. All inter-population crosses were controlled for normality of parents by using them in a simultaneous intra-population cross. The results reported here are a selection from a total of 183 matings involving the genus *Crinia* and representing approximately 7700 eggs.

All measurements were made with a vernier caliper or an ocular micrometer. Range, standard deviation, and standard error of the mean of population samples are presented according to the method of Hubbs and Hubbs (1953).

Parker (1940, pp. 79 and 86) described the variants found in *C. georgiana* and *C. signifera*. Similar variants occur in all granular-bellied species of *Crinia* found in Western Australia and four morphs have been named. They are:

"ridged"—for Parker's *ignita* or *stolata*

"smooth"—for Parker's *affinis*

"lyrate"—for animals with curved ridges over the scapular region

"warty"—for animals with a warty dorsum and lacking ridges

In all polymorphic species it was assumed that various combinations of polymorphs in crosses would be equally viable.

Food habits were determined by examination of the faeces of animals returned and kept in the laboratory.

During this investigation, the calls of breeding males have given important leads in presuming species status. The calls of all *Crinia* species and other Western Australian frogs will be discussed in a later paper.

III. MORPHOLOGICALLY DISTINCT SPECIES

(a) *C. rosea* and *C. leai*

C. rosea and *C. leai* are the only smooth-bellied species of *Crinia* reported from Western Australia. They can be readily identified from Parker's (1940) description. Where the two species are sympatric there are no intergrades, male calls are dissimilar, and ecology is different.

(b) *C. georgiana*

The remaining species of *Crinia* reported from Western Australia differ from the foregoing in having a more or less granular belly. They are *C. georgiana*, *C. glauerti*, and *C. insignifera* (formerly known as *C. signifera*). Parker (1940, p. 81) separates *georgiana* (vomerine teeth usually present) from *signifera* (vomerine teeth vestigial).

Finch (1951) has shown that vomerine teeth are too variable to be useful taxonomically. Of *georgiana* Parker (p. 79) says "Armpit, groins and hinder aspects of the knees brilliant carmine, this colour being fast in alcohol (traces still present after nearly a century) but fugitive in formalin (destroyed in six months)." Of *signifera* he says (p. 86) "orange or carmine on the concealed surfaces of limbs and flanks, these colours being fugitive in alcohol."

In the present investigation more than 70 specimens of *signifera* from eastern Australia have been seen alive; none had red colouring on the leg or thigh. Red-thighed specimens placed in preservative after death lost the red colour of the thigh and groin. No specimen used in matings or killed by being placed in alcohol has lost colour. From this it is taken that specimens which lost colour in alcohol, the "fugitive" of Parker and therefore his *signifera*, were dead for some time prior to being placed in preservative. Specimens which were killed by being placed in formalin failed to retain the full brightness of colour on their thighs and groins. Nevertheless some red colouring did remain.

Breeding males with red thighs had dark throats, white pectoral spots, and similar calls which were distinct from the calls of the males of any other *Crinia*. It was concluded that such males belonged to one species which was *georgiana*.

(c) *C. glauerti*

Parker (1940, p. 81) states "The status of this species is doubtful." In a large measure the doubt is due to Loveridge's (1935, p. 24) statement that *glauerti* is a "miniature form of *georgiana*." Parker rightly points out that some of the characters listed by Loveridge as characterizing *glauerti* are characters of *signifera* rather than *georgiana*. He states further "they have the appearance of small examples of *georgiana*, though having been fixed in formalin it is not possible to say whether the characteristic red on the legs of that species was also present."

Reference to Loveridge's original description shows that the type is a female "marbled beneath". Field experience with red-thighed frogs, here called *georgiana*, shows that females of this species are always white beneath and never coloured or marked beneath in any way. It seems necessary therefore to see if it is possible to determine what Loveridge understood as being *georgiana*.

A clue is given by Loveridge (1935, p. 26) when discussing whether *signifera* or *georgiana* occurs on Rottnest I. Loveridge quotes correspondence with Mr. L. Glauert, Director, Western Australian Museum, of which the following is the final sentence, "From this absence of red I feel certain that Mr. Glauert's specimens were not *C. signifera ignita* but what I understand as *georgiana*." It is clear from this that Loveridge's concept of *georgiana* is exactly opposite to that of Parker.

The type locality of *glauerti* is Mundaring Weir where field collecting shows that *leai*, *georgiana*, and *glauerti* (as determined by marbled-bellied females) are present. *C. leai* cannot be confused with the other species. *C. georgiana* males and females have red thighs, the females are white beneath, the males have a dark throat, white pectoral spots, and call rather like a duck quacking. *C. glauerti* females are marbled beneath, lack red colouring, are never as large as *georgiana* females, and

are associated with small males lacking red colouring but having a dark throat with white pectoral spots and a characteristic call (which can best be likened to a prolonged rattle caused by a pea falling into a can and bouncing). These males are always much smaller than *georgiana* males. The sizes of female and male *glauerti* determined by the foregoing methods falls close to that given by Loveridge ($\delta\delta$ 14.5–15.5 mm; $\varphi\varphi$ 20.5 mm).

(d) *C. insignifera*

This species was established by Moore (1954) on the basis of biological data. Moore gives no description of his type specimen which he states came from Armadale. In correspondence, Moore advised as follows:

- (i) The types of *insignifera* agree with the description and photographs of a *Crinia* known by the present author as the Coastal harsh voice (*Chv*) race and were not *glauerti*.
- (ii) He was unaware of the difference between Attadale and Armadale and he now believed that his specimens came from Attadale.

It was concluded that *insignifera* was synonymous with the *Chv* race and could be distinguished from all other named species of *Crinia* because males have only the chin dark while females lack the bold mottling of *glauerti* females and have the belly lightly flecked in grey.

IV. SIBLING SPECIES

With the exception of *insignifera*, the males of all the morphological species discussed in the previous section have distinct and characteristic calls. *C. insignifera* is composed of three morphologically indistinguishable allopatric populations which can only be characterized by the call of the male. Prior to the receipt of Moore's (1954) paper these call-types had been regarded as "races" and identified by reference to their calls, soil preference, and geographical range. Thus in the region of Perth the ranges of the races are delimited from west to east as follows: the typical *insignifera* (*Chv*) race of the sandy swamps of the coastal plain which dry out in summer; the clay (*Cc*) race found in the clay, summer-dry swamps which form a narrow strip along the front of the Darling Scarp; the Plateau harsh voice (*Phv*) race, found on the Darling Scarp and the plateau to the east of this (see Fig. 1).

Field collecting shows that the call characteristic of typical *C. insignifera* grades, in some localities abruptly and in others in a more gradual manner, into the typical "cheeps" of the *Cc* race. The call change indicates gene flow between the typical *Chv* and the *Cc* race and that these are two races of one polytypic species which is *C. insignifera*.

The call of the *Phv* race remains unchanged from Dongara (200 miles north of Perth) to Esperance (400 miles south-east of Perth). The range of this "race" adjoins that of the two "races" of *insignifera* along a line running from the Moore R. (north of Gingin) through Gingin, then south along the Darling Scarp to the Preston R. where the boundary swings westward to Cape Naturaliste. Across this boundary, calls change abruptly, and no intergrading calls have been found. Several individual calls have been heard which lack the characters of the calls of any of the races and,

since these isolated calls occur in areas where the habitat has changed due to man's activities, they have been regarded tentatively as of hybrid origin.

The field data have been interpreted as indicating that the *Phv* race is a homogenous population because the male call is constant throughout the geographical range. Since the call does not intergrade with either of the other races of *insignifera* it is concluded that no gene flow exists between *insignifera* and the *Phv* race, which is to be regarded as a valid species reproductively isolated from *insignifera* (this presumption was tested by means of *in vitro* crosses as discussed in the following Section).

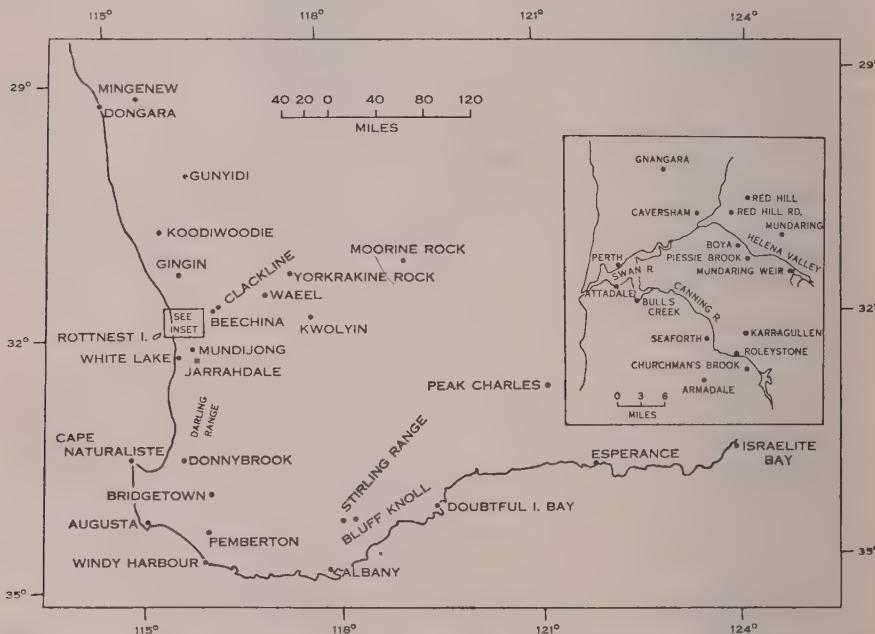


Fig. 1.—Map of south-western Australia showing the principal localities mentioned in the text.

In eastern Australia, specimens have been collected in the Mt. Lofty and Flinders Ranges and Eyre Peninsula of South Australia in December 1952, at Sydney, Urbenville (northern New South Wales), and Mt. Lofty Ranges in December 1954, and in the Murray Valley and Wimmera (Vic.) in August 1955.

During the visits of December 1952 and 1954 specimens agreeing in call and morphology with *signifera* were the only *Crinia* collected. However, the visit to the Murray Valley in August 1955 resulted in the collection of a *Crinia* whose call and morphology was indistinguishable from the Western Australian *Chv* race of *insignifera*. This call-type was not present 10 miles east of Truro, S.A., where *signifera* occurred, but was present at Blanchetown and Kingston-on-Murray (S.A.), and Mildura and Warracknabeal (Vic.). Seven miles north of Horsham (Vic.) *signifera* and the new call-type were found together in the same pond. South of this point *signifera* alone occurred.

A collection was made at the Horsham site and it was soon apparent that the two call-types were distinct and that no intermediate calls were present. The only male specimens taken at this site were those which, prior to being caught, were actually seen to call so that before any thorough attempt was made to identify animals they were grouped according to the call of the male. These two call-types were kept in separate containers for use in experimental crosses.

V. HYBRIDIZATION EXPERIMENTS

The populations recognized in the preceding Sections and thought to be species because of differences in morphology or male call have been checked by a series of *in vitro* crosses, the results of which are given below.

TABLE 1
RESULTS OF CROSSES BETWEEN *C. GEORGIANA* FROM WIDELY SEPARATED LOCALITIES IN
WESTERN AUSTRALIA

Cross No.	♀ Locality	♂ Locality	No. of Eggs	Result
117	Bull's Creek	Bluff Knoll	34	25 (73.5%) hatched, 9 metamorphosed
119	Bull's Creek	Roleystone	25	21 (84%) hatched, 9 metamorphosed
120	Roleystone	Bluff Knoll	25	18 (72%) hatched, 9 metamorphosed
199	Roleystone	Doubtful I. Bay	21	14 (66%) hatched, all lost before metamor- phosis

Because of the difficulty of obtaining gravid females no experimental matings were made between *rosea* and *leai*. Eggs of the granular-bellied species of *Crinia* which had been crossed with *leai* males, always failed to divide. *C. georgiana* eggs crossed with *insignifera* or *glauerti* did not develop beyond blastula. Red-thighed frogs from the same geographical area, irrespective of size or polymorph pattern, produced normal larvae in *in vitro* crosses. Crosses of *georgiana* from geographically widely separated localities produced results as shown in Table 1. It is concluded that red-thighed frogs in Western Australia belong to one species which is *georgiana*.

C. glauerti in Western Australia and *signifera* in eastern Australia are allopatric. Parker (1940, p. 81) points out that these have numerous morphological features in common. Also, the throats and calls of males are very similar. Table 2 lists results of crosses between *glauerti* and *signifera*. They may be summarized as follows:

- (i) Female *glauerti* crossed to male *signifera* from mainland Australia show high viability.
- (ii) Female *glauerti* crossed to *signifera* from Tasmania show marked inviability.

(iii) Female *signifera* from New South Wales when crossed to male *glauerti* produced grossly abnormal embryos.

The first of these results suggests that taxonomic separation is not warranted. On the other hand, the last indicates that valid species status ought to be given. Moore (1954, p. 69) has shown that Tasmanian specimens of *signifera* are fully viable with Sydney specimens and thus the second result is rather unexpected. However, it is consistent with *glauerti* being regarded as a valid species.

TABLE 2
RESULTS OF CROSSES BETWEEN *C. GLAUERTI* AND *C. SIGNIFERA*

Cross No.	♀ Species and Locality	♂ Species and Locality	No of Eggs	Result
210	<i>glauerti</i> Bulls' Creek, W.A.	<i>signifera</i> Port Hacking, N.S.W.	55	89% hatched, 4 larvae with bent tails, remainder normal
211	<i>glauerti</i> Bull's Creek	<i>signifera</i> Port Hacking	49	All hatched, none abnormal
249	<i>signifera</i> E. Lindfield, N.S.W.	<i>glauerti</i> Helena Valley, W.A.	19	11 exogastrulate, 8 proceeded to tail bud but extremely abnormal, only 2 hatched
252	<i>signifera</i> E. Lindfield	<i>glauerti</i> Helena Valley	18	All normal to blastula stage then 9 failed (4 failed to include yolk, 5 reached the neural plate stage), only one hatched, apparently normal
259	<i>glauerti</i> Bull's Creek	<i>signifera</i> Hobart, Tas.	42	Cleavage irregular. By gastrulation 37 had failed, only 5 hatched, 2 with bent tails, 3 apparently normal
373	<i>glauerti</i> Bull's Creek	<i>signifera</i> Horsham, Vic.	37	7 failed at blastula stage, 30 hatched, 1 with bent tail, others apparently normal

Table 3 lists crosses between *glauerti* from Moore's locality at Armadale, *insignifera* from Attadale, and *glauerti* from Bull's Creek, which is only 2 miles from Attadale and from which *glauerti* is easy to obtain. Crosses 178 and 180 show that *glauerti* from Armadale and Bull's Creek are conspecific, while the other matings listed show that *glauerti* from Armadale and Bull's Creek is not conspecific with *insignifera* from Attadale.

TABLE 3

RESULTS OF CROSSES BETWEEN *C. GLAUERTI* FROM ARMADALE AND BULL'S CREEK, W.A., AND TYPICAL *C. INSIGNIFERA* FROM ATTADALE, W.A.

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Result
178	<i>glauerti</i> Armadale (Moore's loc.)	<i>glauerti</i> Bull's Creek	60	92% hatched as normal larvae
180	<i>glauerti</i> Bull's Creek	<i>glauerti</i> Armadale (Moore's loc.)	36	80% hatched as normal larvae
185	<i>glauerti</i> Armadale (Moore's loc.)	<i>insignifera</i> Attadale	45	32 embryos failed to include yolk, these proceeded to neuralation and then cytolized, none hatched as larvae
188	<i>glauerti</i> Armadale (Moore's loc.)	<i>insignifera</i> Attadale	70	24 cytolized by early gastrula, 46 produced exogastrulate embryos which did not develop further, 1 apparently normal embryo developed to rotation, none hatched
183	<i>glauerti</i> Bull's Creek	<i>insignifera</i> Attadale	27	Abnormalities appeared by the 4th cleavage. Others which reached blastulae had begun to cytolize. 9 were exogastrulated and retarded, 5 of these became oedematous larvae with short tails
184	<i>glauerti</i> Bull's Creek	<i>insignifera</i> Attadale	31	All which reached gastrulation had extruded yolk, 23 produced exogastrulate embryos which reached neural fold stage, none hatched
186	<i>glauerti</i> Bull's Creek	<i>insignifera</i> Attadale	44	36 embryos failed to include yolk, reached head and tail stage in development, but then cytolized

Table 4 shows the result of a cross between *insignifera* from Attadale and *signifera* from East Lindfield (N.S.W.). It is consistent with the result of Moore's first New South Wales \times Western Australia cross (Moore 1934, p. 70).

Results of crosses between the three races of *insignifera* are listed in Table 5. The *in vitro* crosses do not give a clear answer as to the species status of these forms, apparently-similar matings giving contradictory results (e.g. crosses Nos. 137 and 139). These crosses differ, apart from geographically different origins of the females, as follows: cross No. 137 is between polymorphs lyrate \times lyrate, while cross No. 139 is between polymorphs ridged (striped) \times ridged. It is possible that there is a differential viability between various polymorphs, but cross No. 111 is between polymorphs ridged \times ridged and is inviable while crosses Nos. 114 and 112, in which the same female was used, are each ridged \times lyrate, cross No. 100 is lyrate \times lyrate, and cross No. 130 is lyrate \times smooth, all of which are viable.

TABLE 4
RESULTS OF CROSS BETWEEN TYPICAL *C. INSIGNIFERA* AND *C. SIGNIFERA*

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Result
244	<i>signifera</i> East Lindfield, N.S.W.	<i>insignifera</i> Attadale, W.A.	43	3 embryos hatched, tails short and bent, gut walls ruptured, none normal; others cytolized in blastula or gastrula stages

It thus seems that differential viability between polymorphs cannot explain the variability in the results from matings between the *Chv*, *Phv*, and *Cc* call-types. The populations are allopatric and the call of the *Phv* race does not intergrade with any other call-type from which it is concluded that the *Phv* race is a valid species. From the results of crosses listed in Table 5 it is clear that genetic isolation is not yet as far advanced as between *insignifera* and *glauerti* in which uniform results for successive replications of matings is possible, e.g. the crosses *glauerti* female \times *insignifera* male (Table 3).

Table 6 gives the results of crosses between *glauerti* and *insignifera* which are additional to those listed in Table 3. Table 6 also includes the results of crosses between *glauerti* and the *Phv* race which are not different from those of *glauerti* by *insignifera*. The results indicate that the *Phv* race is not conspecific with *glauerti*. The three crosses in Table 7 indicate that the *Phv* race is not conspecific with *signifera*. It thus seems that the *Phv* race is a valid species and in want of a name. The species is described in the next Section.

As stated above, field collecting in eastern Australia revealed the presence of a population having similarities in morphology and male call with typical *insignifera*. This population occurred with typical *signifera* at Horsham, Vic. At this site only two females were taken despite an intense search. One of the females agreed in belly-colour pattern with *signifera*. The other lacked the belly characteristics of *signifera* and was presumed to be the female of the new form. Unfortunately this animal did not have eggs in the oviduct and was thus unsuitable for experimental use. The *signifera* female did have eggs in the oviduct and was used for *in vitro* crosses with the results as presented in Table 8.

The reciprocal cross may show marked inviability similar to that shown by the reciprocal crosses of *glauerti* by *signifera* (Table 2) or *glauerti* by *insignifera* (Tables 3

TABLE 5
RESULTS OF CROSSES BETWEEN THE COASTAL (*Chv*) AND CLAY (*Cc*) RACES OF *C. INSIGNIFERA*
AND CRINIA (*Phv*) SP. FROM WESTERN AUSTRALIA

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Result
46	<i>insignifera</i> (<i>Chv</i>) Gingin	<i>insignifera</i> (<i>Cc</i>) Caversham	36	44% hatched as apparently normal larvae
164	<i>insignifera</i> (<i>Chv</i>) Attadale	<i>Crinia</i> (<i>Phv</i>) sp. Waeel	35	63% hatched as apparently normal larvae
166	<i>insignifera</i> (<i>Chv</i>) Attadale	<i>Crinia</i> (<i>Phv</i>) sp. Beechina	42	83% hatched as normal larvae
111	<i>insignifera</i> (<i>Cc</i>) Caversham	<i>insignifera</i> (<i>Chv</i>) Rottnest I.	32	None developed normally, 3 only hatched, and these had small heads, swollen bodies
114	<i>insignifera</i> (<i>Cc</i>) Caversham	<i>insignifera</i> (<i>Chv</i>) Attadale	30	26% hatched, apparently normal
112	<i>insignifera</i> (<i>Cc</i>) Caversham	<i>Crinia</i> (<i>Phv</i>) sp. Clackline	28	64% hatched, apparently normal
100	<i>Crinia</i> (<i>Phv</i>) sp. Red Hill	<i>insignifera</i> (<i>Chv</i>) Rottnest I.	22	55% hatched, apparently normal
137	<i>Crinia</i> (<i>Phv</i>) sp. Beechina	<i>insignifera</i> (<i>Chv</i>) Rottnest I.	30	7% hatched, apparently normal
139	<i>Crinia</i> (<i>Phv</i>) sp. Yorkrakine Rock	<i>insignifera</i> (<i>Chv</i>) Rottnest I.	54	91% hatched, apparently normal
140	<i>Crinia</i> (<i>Phv</i>) sp. Yorkrakine Rock	<i>insignifera</i> (<i>Cc</i>) W. Armadale	34	41% hatched, apparently normal
141	<i>Crinia</i> (<i>Phv</i>) sp. Yorkrakine Rock	<i>insignifera</i> (<i>Cc</i>) Seaforth	41	81% hatched, apparently normal
130	<i>Crinia</i> (<i>Phv</i>) sp. Beechina	<i>insignifera</i> (<i>Cc</i>) Caversham	94	Normal until late blastula by which time 27 embryos had failed; remaining 67 produced exogastrulate embryos, all cytolized

and 6) but there was no opportunity to make this cross. Because of the indecisive nature of the results achieved in these crosses all the larvae were kept in an attempt to

rear them to metamorphosis. The larvae of both experimental crosses soon showed developmental defects and, in both, a very large number of larvae did not grow at all. These animals were so difficult to keep alive that only 13 survived in the first cross of Table 8. All of these were normal. In the second cross, 34 survived of which only nine were normal. It seems that there is a marked reproductive barrier between the two populations and, in regard to *signifera*, the other population is behaving as a valid species; it is described as such in Section VI.

TABLE 6
RESULTS OF CROSSES BETWEEN *C. GLAUERTI*, THE TWO *C. INSIGNIFERA* RACES, AND *CRINIA (Phv)*
SP. FROM WESTERN AUSTRALIA

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Result
51	<i>insignifera (Chv)</i> Gingin	<i>glauerti</i> Red Hill	29	38% hatched, apparently normal
52	<i>insignifera (Chv)</i> Gingin	<i>glauerti</i> Red Hill	28	68% hatched, apparently normal
315	<i>insignifera (Cc)</i> Seaforth	<i>glauerti</i> Bull's Creek	184	Only 29 (16%) hatched; these had bent tails and small heads
42	<i>Crinia (Phv)</i> sp. Koodiwoodie	<i>glauerti</i> Red Hill	32	72% hatched, apparently normal
104	<i>Crinia (Phv)</i> sp. Red Hill	<i>glauerti</i> Red Hill	13	61% hatched, normal
133	<i>Crinia (Phv)</i> sp. Beechina	<i>glauerti</i> Bull's Creek	59	57% hatched as apparently normal larvae
237	<i>glauerti</i> Bull's Creek	<i>Crinia (Phv)</i> sp. Moorine Rock	20	2 cytolized in blastula, 18 exogastrulate embryos, none hatched

A number of males of this new species were returned to Perth from the Kingston-on-Murray site and several males of both species were returned from the Horsham site. When these specimens arrived in Perth in September, the season was a little too advanced to get a large series of females of the local species. However, it was possible to make some crosses. Males of *signifera* from Horsham when crossed to *glauerti* produced a high percentage of apparently normal larvae (cross No. 373, Table 2) which agrees with the results of similar crosses between *glauerti* and *signifera* from New South Wales.

Results of crosses between *glauerti* and the new *Crinia* from Horsham and Kingston-on-Murray are given in Table 9. The results leave no doubt that the *Crinia* from Horsham differs from *glauerti*. A number of crosses were made between

topotypes of *insignifera* and the new *Crinia* from Horsham. The two sets of results presented in Table 10 indicate a high degree of inviability which is unexpected in

TABLE 7
RESULTS OF CROSSES BETWEEN *C. SIGNIFERA* AND *CRINIA (Phv)* SP.

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Results
245	<i>signifera</i> E. Lindfield, N.S.W.	<i>Crinia (Phv)</i> sp. Helena Valley, W.A.	44	Early cleavage irregular, 31 failed in blastula, 2 in gastrula; 1 hatched, apparently normal
248	<i>signifera</i> E. Lindfield	<i>Crinia (Phv)</i> sp. Helena Valley	18	Cleavage irregular, none proceeded beyond blas- tula
251	<i>signifera</i> E. Lindfield	<i>Crinia (Phv)</i> sp. Helena Valley	17	All cleaved, none devel- oped beyond blastula

view of the similarities in the calls of the males. The crosses have been taken as indicating that the *Crinia* from Horsham is specifically distinct from *insignifera* from Western Australia.

TABLE 8
RESULTS OF CROSSES BETWEEN TYPICAL *C. SIGNIFERA* FROM NEAR HORSHAM, VIC., AND AN UNNAMED
SPECIES (CALL-TYPE *Chv*) FROM THE SAME SITE AND FROM KINGSTON-ON-MURRAY, S.A.

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Results
358	<i>C. signifera</i> 7 miles N. of Horsham	<i>Crinia</i> (call-type <i>Chv</i>) sp. 7 miles N. of Horsham	66	24 failed by late blastula, slightly retarded com- pared with controls; 41 (62%) hatched, appar- ently normal
359	<i>C. signifera</i> 7 miles N. of Horsham	<i>Crinia</i> (call-type <i>Chv</i>) sp. Kingston-on-Murray	88	23 failed in early and late blastula, retarded com- pared with controls, neural folds irregular; 61 (69%) hatched, ap- parently normal

Results of crosses presented earlier (Tables 5 and 6) and field observations have indicated that the *Phv* race is specifically distinct from other western populations. Despite the dissimilarities in the calls of males, two crosses were made between females

of the *Phv* race and males of the *Crinia* from Horsham. The results are presented in Table 11. The very small numbers of eggs used were all that could be obtained

TABLE 9

RESULTS OF CROSSES BETWEEN *C. GLAUERTI* FROM WESTERN AUSTRALIA AND *CRINIA* (CALL-TYPE *Chv*) SP. FROM HORSHAM, VIC., AND KINGSTON-ON-MURRAY, S.A.

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Results
376	<i>glauerti</i> Attadale	<i>Crinia</i> (call-type <i>Chv</i>) sp. Kingston-on-Murray	46	Very retarded, 13 reached yolk plug stage, none proceeded further
380	<i>glauerti</i> Bull's Creek	<i>Crinia</i> (call-type <i>Chv</i>) sp. Kingston-on-Murray	24	3 failed in blastula, remain- der failed to include yolk, 2 hatched
382	<i>glauerti</i> Bull's Creek	<i>Crinia</i> (call-type <i>Chv</i>) sp. 7 miles N. of Horsham	29	7 failed in blastula, 10 failed to include yolk, 12 hatched, with small heads, ruptured abdo- men, and bent tails
409	<i>glauerti</i> Karragullen	<i>Crinia</i> (call-type <i>Chv</i>) sp. Kingston-on-Murray	23	All failed to include yolk
411	<i>glauerti</i> Karragullen	<i>Crinia</i> (call-type <i>Chv</i>) sp. 7 miles N. of Horsham	10	All failed to include yolk
418	<i>glauerti</i> Pickering Brook	<i>Crinia</i> (call-type <i>Chv</i>) sp. Kingston-on-Murray	45	4 failed in blastula, re- mainder failed to include yolk

TABLE 10

RESULTS OF CROSSES BETWEEN TYPICAL *C. INSIGNIFERA* FROM WESTERN AUSTRALIA AND *CRINIA* (CALL-TYPE *Chv*) SP. FROM HORSHAM, VIC., AND KINGSTON-ON-MURRAY, S.A.

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Results
385	<i>insignifera</i> Attadale	<i>Crinia</i> (call-type <i>Chv</i>) sp. Kingston-on-Murray	18	Many failed in blastula, only 3 hatched, appar- ently normal
386	<i>insignifera</i> Attadale	<i>Crinia</i> (call-type <i>Chv</i>) sp. 7 miles N. of Horsham	18	None proceeded beyond blastula

because of the lateness of the season. The results indicate that the *Crinia* from Horsham is reproductively isolated from the *Phv* race.

In summary, the crosses of Tables 8, 9, 10, and 11 indicate that the *Crinia* from Horsham, having a call like the *Chv* race of *insignifera*, is reproductively isolated from *signifera*, *insignifera*, *glauerti*, and the *Phv* race from Western Australia.

TABLE 11

RESULTS OF CROSSES BETWEEN CRINIA (*Phv*) SP. FROM WESTERN AUSTRALIA AND CRINIA (CALL-TYPE *Chv*) SP. FROM KINGSTON-ON-MURRAY, S.A.

Cross No.	♀ Species and Locality	♂ Species and Locality	No. of Eggs	Results
421	<i>Crinia (Phv)</i> sp. Pickering Brook	<i>Crinia (call-type Chv)</i> sp. Kingston-on-Murray	15	2 failed to cleave; all those cleaving retarded when compared to control, those which proceeded to neuralation had extruded yolk; only 5 hatched with small heads, bent tails, and yolk plugs
424	<i>Crinia (Phv)</i> sp. Helena Valley	<i>Crinia (call-type Chv)</i> sp. Kingston-on-Murray	13	5 failed in blastula, 1 failed at dorsal lip, 2 failed in gastrulation; 5 hatched, apparently normal

VI. SYSTEMATICS AND BIOLOGY

Parker (1940) cites all the literature and this will not be repeated; instead reference is made to the relevant parts of Parker's paper for the synonymy. The specimens listed as examined were those collected by the author and are now in the Zoology Department Collection, University of Western Australia.

Genus CRINIA Tschudi

Crinia Tschudi, 1838, Mem. Soc. Neuchâtel. Sci. Nat. 2: 38, 78; Parker, 1940, Novit. Zool. 42: 71.

Type species *Crinia georgiana* Tschudi, 1838.

CRINIA ROSEA Harrison

Crinia rosea Harrison, 1927, Rec. Aust. Mus. 15: 279; Parker, 1940, op. cit. p. 74; Main, 1954, W. Aust. Nat. 4: 122.

Diagnosis.—Resembles *leai* but stouter, with much shorter hind legs, which when measured from anus to tip of longest toe are 1·1–1·36 the length of the body, as against 1·36–1·64 for the same ratio in *leai*. The pink belly colour is distinctive, may vary from pale brown to almost black dorsally, pale animals frequently having a variable dark stripe commencing between the eyes and running posteriorly, may be emarginate backwards of the scapular region. Other details as in Parker (loc. cit.). Mean length for males 22·71±1·70 mm, for females 24·8 mm.

Type locality.—Pemberton.

Specimens examined.—Pemberton, 11 ♂♂, 1 ♀; Dombakup, 3 ♂♂, 1 ♀.

Range.—Restricted to very wet karri (*Eucalyptus diversicolor* F.v.M.) forest. Specimens have been heard calling, but have not been collected, at Northcliffe, which lies in an adjacent river-drainage system 20 miles south of the type locality.

Habitat.—Dense wet thickets beside streams. In January it has been taken from the vacant burrows of *Chaurops* sp. in the banks of East Brook. Because of larval requirements it is unlikely that this frog will be found outside very wet forest country.

Biology

Voice.—Repetitive metallic clicking. These frogs will call back if one imitates the call by clicking the tongue against the roof of the mouth, the repetition frequency appearing to be important for obtaining a response. The time when males commence to call is not known, they have been heard calling in September and at the end of October. They call from a depression which has been made by the animal and which is about 25/35 mm and 8 mm deep. Air temperature when species have been heard calling ranges from 12 to 14°C.

Life history.—Clasping pairs have not been taken in the field but more than 30 egg masses have been examined. These invariably occupy a depression which is presumed to be the one occupied by the calling male. Egg masses have been found in soil beneath grass (trout hatchery) and in the centre of a rotten marri (*E. calophylla* R.Br.) log (Dombakup). This last situation was a log about 20–25 ft long and about 2 ft in diameter, the central 10–12 ft being occupied by a bull-dog ant (*Myrmecia* sp.) colony. The two ends of the log revealed a total of 19 egg masses, while some depressions were still occupied by males. The eggs all appeared to be at the same stage of development with the egg membranes broken down and the pale long-tailed tadpoles free in the jelly.

From the situation in which all egg masses have been found it could not be possible for the larvae to spend any of their life in water. Specimens returned to the laboratory have completed their development and metamorphosed successfully when kept in a saturated atmosphere and left within the depression in the soil as found. During this period the larvae lie passively within the broken down egg capsules. Specimens move infrequently, stimulus by touch elicits a very slight response. Egg masses vary from 26 to 32 eggs and in those masses returned to the laboratory no mortality was observed until after metamorphosis. The mean yolk diameter of eggs is 2.35 mm.

Eggs in which development had proceeded some way before collection completed metamorphosis in from 37 to 56 days in the laboratory at a constant temperature of 16°C. Larvae collected at Dombakup on September 28, 1954, completed development on November 3, 1954. Others collected in the previous season, October 27, 1953, took until December 22 of that year to metamorphose, but these embryos were at a much earlier stage than the Dombakup specimens so it seems that larval life in the field, i.e. from egg to metamorphosis, may be over 60 days.

The larvae of this species are easily identified because of their occurrence in the broken down egg capsules away from water. At the stage of hind limb development (Fig. 2(g)) they average 15.8 mm long and 2.5 mm deep; the operculum is not conspicuous, nostrils relatively large, mouth not open, and lip teeth not apparent. At metamorphosis juveniles are 6.0 mm long.

Food.—Large quantities of sand and sludge have been recovered from faeces and, in addition, one annulation of a diplopod has been found. It is possible that the main diet may be earthworms or other soft-bodied invertebrates.



Fig. 2.—*Crinia* tadpoles: (a), (b) *georgiana*; (c), (d) *leai*; (e), (f) *glauerti*; (g) *rosea*; (h) *pseudinsignifera*.

CRINIA LEAI Fletcher

Crinia leai Fletcher, 1898, Proc. Linn. Soc. N.S.W. 22: 677. Parker 1944, sp. nov. p. 78.
Main, 1954, op. cit. p. 123.

Diagnosis.—Lacks the red-on-belly characteristic of *rosea*; has much longer legs than *rosea*. The toes of *leai* are dilated at the tip as noted by Parker and this appears to be related to its life among reeds in and adjacent to water. May have large yellow spots scattered over the dorsum, otherwise as described in Parker (loc. cit.). Length from snout to anus for a series of mature animals from the Armidale area (near to the northern extent of the range) 21.97–23.37 mm. There is no pronounced sexual dimorphism and females are not readily distinguished from males.

Type locality.—Bridgetown; Pipe Clay Creek, near Jarrahdale.

Specimens examined.—Mundaring, 4 ♂♂, 1 juv.; Karragullen, 1 ♂; Armidale, 1 ♂; Churchman's Brook, 6 ♂♂; Karragullen, Pickering Brook Rd., 1 ♂; Jarrahdale, 3 ♂♂; Albany Rd., Jarrahdale turnoff, 28 ♂♂, 1 ♀, 2 juvs.; Albany Bridge, 6 ♂♂, 2 juvs.; Lake Leppington, 1 ♂, 3 juvs.; Porongorups, 7 ♂♂; Walpole, 3 ♂♂; Karragullen, Narrows Rd., 1 ♂; Narrows Rd., 22 ♂♂; Deep River, 7 ♂♂; Pemberton, 6 ♂♂, 2 ♀♀, 2 juv.

Range.—As far north as Mundaring. Appears to be restricted to the valleys of the Darling Scarp, not found on the Swan coastal plain. The eastern limit of the range is Mundaring, and a line running south from this point parallel to edge of the scarp limits the eastern extent. In the south, the range extends from Gipsy Lagoon to

Albany with a northern outlier in the Porongorups, not taken east of these last two localities.

Habitat.—Favours moist, swampy, shaded places, in which grass and reeds are common. Much commoner in the south of its range which is presumably related to the greater abundance of water in the south.

Biology

Voice.—A high pitched "tk", "tk", "tk", . . . the call being sometimes confused with that of a typical *C. insignifera*. Males commence calling in April and have been heard calling as late as October 27. Males call from about water level from among reeds and similar tussocky plants growing in or at the edges of water.

Life history.—Eggs are stuck in clumps above water level among reeds and tussocks as early as April and, in the south of the range, similar masses have been seen in June (Porongorups) and September (Pemberton). They contain from 52 to 96 eggs. Dimensions are as follows: capsule about 4 mm in diameter, yolk from 1.66 to 2.03 mm in diameter. The eggs of individual masses show little variation in size.

Eggs collected at Pemberton on April 18, 1954, when at the first or second cleavage, hatched in 15 days, at which time the mean body length from snout to anus was 2.62 mm with a tail of 5.15 mm. In the field, the hatching larvae wriggle from the suspended egg mass and fall into the water beneath. Larvae hatched from a Roleystone egg mass were 2.75 and 3.89 mm long for body and tail respectively.

Specimens reared from egg masses returned to the laboratory metamorphosed in from 149 to 174 days. Tadpoles may be identified from Figures 2(c), 2(d). At the stage shown in the figure larvae are 24–27 mm long of which the body is 9–10 mm, brown, with large clear spaces anterior to the eyes and laterally just behind the eyes. Spiraculum clearly visible from above, just visible ventrally. Lip teeth are variable with a formula from $\frac{1}{1}-\frac{1}{1}$ to $\frac{1}{3}-\frac{1}{1}$. The anus opens to the right and is not on a tube.

Larvae metamorphose in the field in late October (Mundaring); at this time laboratory-reared animals were also metamorphosing. Young frogs have the broad dorsal stripe characteristic of the species although in some specimens it is already eroded posteriorly.

Juveniles at metamorphosis are 9–10 mm long. Small non-breeding specimens at the commencement of winter are 13–16 mm, and small breeding adults are 18–19 mm. It is probable that sexual maturity is reached in the second year after metamorphosis.

Food.—Food remains from faeces are mostly unidentifiable. Diet is probably small flying insects.

CRINIA GEORGIANA Tschudi

Crinia georgiana Tschudi, 1838, Mem. Soc. Neuchâtel. Sci. Nat. 2: 38, 78; Parker, 1940, op. cit. p. 78; Main, 1954, op. cit. p. 123.

Diagnosis.—Sexually mature frogs have red on limbs. This coloration is lost if the specimen is dead for some time before being placed in alcohol. The hind leg/body ratio of this and the following species falls within the range already given for *C. leai*. The dorsal colour pattern and skin texture varies widely as discussed by Parker (1940, pp. 79 and 80).

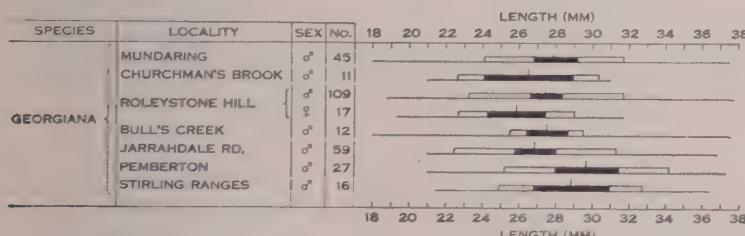


Fig. 3.—*C. georgiana*: total lengths, plotted by the method of Hubbs and Hubbs (1953). For each locality the range is shown by a heavy horizontal line; the mean (M) by a short vertical line. The blackened part of each bar comprises two standard errors of the mean ($2\sigma_m$) on either side of M . One-half of each black bar plus the white bar at either end outline one standard deviation (σ) on either side of M .

Sexually mature animals are from 18 to 38 mm. Statistics of population samples shown in Figure 3, these are given from north at the top to south of the range at the bottom; there is no trend with change of latitude. The same figure shows that the mean size of females is the same as or less than that of males. In this character this species differs from other *Crinia* species examined in which females are always larger than males.

Type locality.—King George Sound.

Specimens examined.—Gingin, 2 ♂♂, 2 ♀♀; Walyunga, north of, 3 ♂♂; Gidgegannup, 1 ♂; Brockman R., 1 ♂, 2 ♀♀; Red Hill, 1 ♂; Victoria Dam, 2 ♂♂, 2 ♀♀; Darlington, 1 ♂; Bickley Camp, 4 ♂♂; Armadale, 3 ♂♂; Churchman's Brook, 11 ♂♂; Cobbler's Pool (Roleystone), 6 ♂♂; Roleystone Hill, 109 ♂♂, 17 ♀♀; Canning Bridge, Roleystone Hill, 9 ♂♂; Mundaring, 45 ♂♂, 4 ♀♀; Albany Rd., Jarrahdale turnoff, 2 ♂♂; Bull's Creek, 12 ♂♂, 1 ♀; Jarrahdale, 59 ♂♂; Boyanup-Dardanup Rd., 1 ♂; Middlesex, 1 ♀; Pemberton, 26 ♂♂; Windy Harbour, 2 miles north of, 4 ♂♂; Augusta, 4 miles north of, 2 ♂♂; Karridale-Nannup Rd., 3 ♂♂; Shannon Mill, 3 ♂♂, 1 ♀; Stirling Ranges, 16 ♂♂, 8 ♀♀; Cheyne Beach, 2 ♂♂; Bremner Bay, 1 ♂; Doubtful Island Bay, 1 ♀.

Range.—As for *leai* with the addition that it extends on to the coastal plain where there is permanent moisture throughout the summer. The northern limit is near Gingin. The southern part of the range includes the Stirling Ranges where *leai* has not been found and then along the south coast to Esperance. It has not been collected, and is presumed not to be present, in the soaks north of Israelite Bay. Does not occur on Rottnest I.

Habitat.—In vegetation along permanent streams and soaks. Specimens have been taken at 2200 ft on Mt. Hassell (Stirling Ranges).

Biology

Voice.—A loud distinctive “quack”, “quack”, . . . males which have stopped calling because of the approach of an observer will call again if even a crude imitation

of the call is made. Males commence calling in May as temperatures fall with the approach of winter. They call from a depression just large enough to fit the animal and containing water which is usually not more than $\frac{1}{2}$ in. deep. Males may call on cool, overcast days, but then they are usually covered by a light litter of fallen leaves. Calling ceases in September or October with the rise in temperature and decrease in frequency of rainfall. Males call with air temperatures as high as 15°C but such animals are easily disturbed. Clasping pairs have been collected during frontal rains associated with winter type cyclones and at such times air temperatures ranged from 13–9°C. Strong winds will prevent choruses developing, even when other factors are favourable. Cold easterly winds are worse in this regard.

Life history.—Clasping pairs occupy the depression made and used by the calling male. During daylight, males are surrounded by eggs laid by females with which they have mated. The eggs, larvae, and frogs have not been seen associated with deep waters, i.e. over 4–6 in. in depth. The number of eggs per female is about 70. There may be a slight variation in egg numbers between the various polymorphs. Dimensions of eggs varied as follows; capsule 2·73–4·19 mm in diameter, and yolk 1·73–2·75 mm. Eggs within each egg mass showed little variation and the entire range of yolk diameters was found within the Roleystone population and does not appear to be associated with the size or polymorph characteristics of the female.

At hatching, tadpoles are about 7·0 mm long (body 2·0 mm, tail 5·0 mm). Growth is rapid. Eggs kept at 16°C hatched in from 9 to 12 days and completed metamorphosis 40–46 days after fertilization. Eggs kept at 20°C hatched in 7 days and metamorphosed in 26–28 days. In the field, hatching takes about 7 days and metamorphosis 30–40 days after fertilization. Tadpoles may be identified by reference to Figures 2 (a) and 2 (b) and are characterized by the flat body and very long slender tail. Specimens as figured are about 17 mm long of which 4·75 mm is body. Specimens with well-developed hind limbs are 20·5 mm long just before metamorphosis.

Larvae have a golden sheen on the sides, tail transparent with large white guanophores. Spiraculum not easily visible from above, anus on a short tube opening to the right. Lip-teeth variable, commonly following a $\frac{2}{1} \frac{1}{2}$ formula with the bottom row on the lower lip situated medially, very short, and arched upward in a small crescent.

At metamorphosis animals leave the shallow water and crawl into the moist mud adjacent, usually beneath litter, where they remain with the remnant of the tail still within the water. Juveniles measure from just over 5·0 mm to (rarely) 6·0 mm. The smallest adult successfully used in mating experiments was 18 mm long, and animals smaller than this have not been taken in the field and do not associate with adults in breeding congresses.

Food.—Sand and remains of the following have been recovered from the faeces: snails (*Bothriembryon* and *Luinodiscus*), winged reproductive ants, beetles, *Collembola*, spiders, flies, and mites.

CRINIA GLAUERTI Loveridge

Crinia glauerti Loveridge, 1933, Occ. Pap. Boston Soc. Nat. Hist. 8: 57; Parker, 1940, op. cit. p. 81; Main, 1954, op. cit. p. 124.

Diagnosis.—Female: belly boldly marked in black and white; male: throat dark, white pectoral spots. Range of sizes as in Figure 4. Distinguished from *georgiana* by smaller size and absence of red colouring in groin and on thigh of both sexes. Male

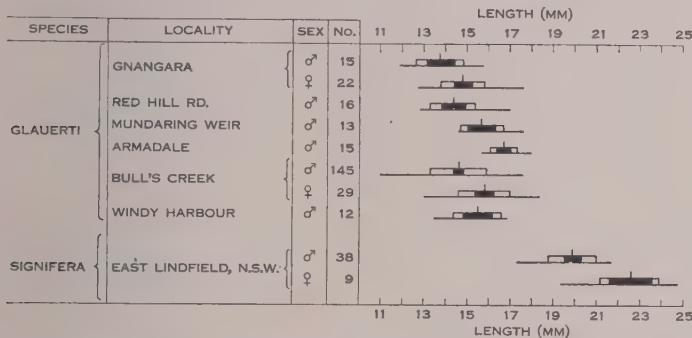


Fig. 4.—Species of the *C. signifera* super-species. Total lengths plotted by the method of Hubbs and Hubbs (1953). For explanation see Figure 3.

distinguished from *insignifera* by dark throat and narrow, pointed head. Sexual dimorphism marked, females larger than males. *C. signifera*, the presumed ancestor, is larger than *glauerti*. The samples suggest that specimens from hill populations may be larger than those of the coastal plain.

Type locality.—Mundaring Weir.

Specimens examined.—Lake Bambum, 10 miles south of, 1 ♀; Gnangara, 15 ♂♂, 22 ♀♀; Red Hill Rd., 16 ♂♂; Walyunga, 1 ♂, 4 juv.; Mundaring, 1 ♀; Mundaring Weir, 13 ♂♂; Churchman's Brook, 3 ♂♂, 1 ♀, immature; Armadale, 15 ♂♂, 4 ♀♀; Helena Valley, 5 ♂♂, 3 ♀♀; Roleystone, 3 ♂♂, 2 ♀♀; Gosnells, 1 ♂, 2 ♀♀; Bull's Creek, 145 ♂♂, 29 ♀♀; Attadale, 4 ♂♂; Bibra Lake, 3 ♂♂; Jarrahdale, 4 ♂♂; Mundijong, 1 ♂; Greenbushes, 1 ♂; Cape Leewin, 1 ♂; Pemberton, 1 ♂; Windy Harbour, 2 miles north of, 11 ♂♂, 5 ♀♀; Deep R. 1 ♂, 3 ♀♀; Nornalup, 1 ♀; Porongorups, 2 ♂♂, 1 ♀; Stirling Ranges, 7 ♂♂, 4 ♀♀; Warriup, 1 ♂.

Range.—As for *georgiana*, except that *glauerti* has not been found at Esperance where *georgiana* has been reported and heard calling. Not on Rottnest I.

Habitat.—Same as *georgiana*—these two species are frequently found together in the same environment. Males of both species call together from shallow water, and larvae of both species are to be found in the same situations. Seepage of water through the summer is essential for the occurrence of this frog. It adapts well to boggy pastures.

Biology

Voice.—A prolonged rattling call. Males will call as early as the middle of March provided temperature and rainfall conditions are favourable. Preferred conditions for mating appear to be the same as those already listed for *georgiana*. Males have not been heard calling in December but if there are showers and cool

nights they may call almost to the end of November. Males will sometimes be heard calling from water up to several feet deep, but on these occasions they are supporting themselves on the stems of watercress (*Nasturtium* sp.) or *Spirogyra*.

Adjacent to Perth the call of this species is constant and is predominantly a rattle, but occasionally a short squelching sound is made. On the south coast where no other *Crinia* except *georgiana* and *leai* are found the squelching call is far more prominent and it was for some time confused with one of the "harsh voice" types of call. However, none of these frogs has been collected on the south coast between Augusta and Albany and *glauerti* has been seen and recorded making both calls.

Life history.—Clasping pairs can be found in the same situations as those occupied by the calling males. Mating usually takes place on the night of rain or on the one immediately following. Females always appear to be scarce as compared with the number of males present.

The number of eggs per female is about 70. Dimensions of eggs range from 1.85 to 2.68 mm for capsule diameter and 0.97 to 1.3 mm for yolk diameter. These values represent ranges of means of 20 eggs from each egg mass examined in the laboratory.

Eggs fertilized in the laboratory hatched in from 9 to 10 days. Mean lengths of freshly hatched larvae ranged from 5.5 to 6.9 mm of which the body is a little over 2.0 mm and the tail the remainder. Larval life is long, larvae kept at 16°C had not completed metamorphosis in 130 days when they died with well-developed hind limbs. Metamorphosing juveniles were taken in the field on October 3 (Bluff Knoll, A. K. Lee) and October 7 (Gnangara, A.R.M.). Juveniles from Bluff Knoll (Stirling Ranges) ranged from 7.0 to 7.5 mm while those from Gnangara ranged from 7.5 to 9.4 mm. Well-grown larvae with fully developed hind limbs taken from this site on October 7 were 24.0 mm long of which 8.0 mm was body, so the 9.4-mm animal above may have grown since metamorphosis.

Tadpoles may be identified by reference to Figures 2 (e) and 2 (f). They are characteristically very dark, unlike the larvae of *insignifera* which is grey and mottled. The specimen figured is 19 mm long, the spiraculum is barely visible or cannot be seen from the dorsal surface. The anus opens to the right but is not characteristic. The lip-teeth offer no means of differentiating between this species and *insignifera*.

This species is noteworthy because at metamorphosis the juvenile is already 50 per cent. of the mean adult size compared with 20–25 per cent. of mean adult size of *georgiana* juveniles. Small adults are often found breeding about September and later and these may represent animals which metamorphosed in the previous season in which case it follows that animals would breed when one year old.

Food.—The following have been found in faeces: wings of Diptera (Simuliidae and Culicidae); beetle elytra; heads of ants (*Rhytidoponera*, *Camponotus*, and *Iridomyrmex*).

CRINIA INSIGNIFERA Moore

Crinia insignifera Moore, 1954, Amer. Nat. 88: 71; Parker, 1940, op. cit. p. 84 (*C. signifera* in part); Main, 1954, op. cit. p. 123 (in part).

Diagnosis.—Male: a broader head and less pointed snout than *glauerti* males. In breeding males the chin only is dark and the throat is white or flecked with brown

while in *glauerti* the throat back to at least the insertion of the arms is black. Pectoral spots are present in *glauerti* but absent or inconspicuous in *insignifera*. The belly may be flecked in grey or black. Female: throat dirty white, belly flecked with small grey or black patches, never boldly mottled as in female *glauerti*. Dimensions of males and females are shown in Figure 5 and the means of males and females from Attadale (i.e. topotypes) are 14.1 and 19.7 mm respectively.

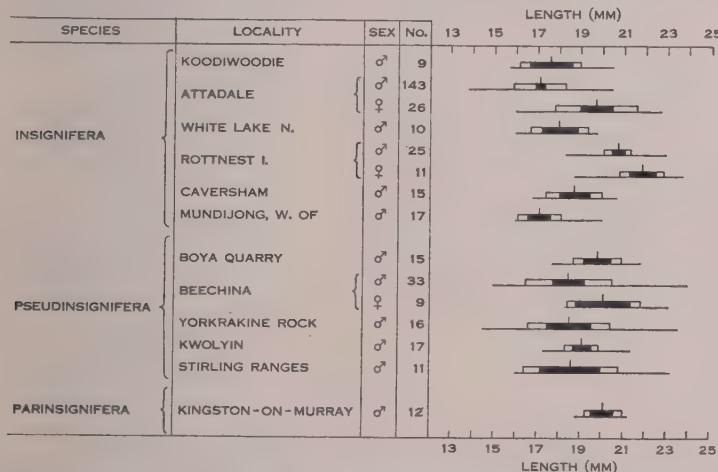


Fig. 5.—Species of the *C. insignifera* super-species. Total lengths plotted by the method of Hubbs and Hubbs (1953). For explanation see Figure 3.

Type locality.—Armadale, subsequently changed to Attadale (Moore, *in litt.*, Jan. 13, 1955).

Specimens examined.—Gingin, 5 ♂♂; Lake Bambum, 5 ♂♂, 3 ♀♀; South Belmont, 1 juv.; Attadale, 143 ♂♂, 26 ♀♀; Bibra Lake, 1 ♀; White Lake (north), 10 ♂♂, 1 ♀; Rottnest I., 25 ♂♂, 11 ♀♀; Canning Vale, 3 miles south of, 1 ♂, 1 ♀; between Myalup and Australind, 1 ♂; Woodlupine Brook, 2 ♀♀; Caversham, 15 ♂♂, 3 ♀♀; Mundijong, and west of, 17 ♂♂, 2 ♀♀; Seaforth, 7 ♂♂; Armadale (west), 8 ♂♂, 5 ♀♀; between Boyanup and Dardanup, 2 ♂♂.

Range.—Within the area bounded by the Moore R. in the north, the Darling Range in the east, and a line joining Donnybrook and Cape Naturaliste in the south. A population of the *Chv* race is found on Rottnest I.

Habitat.—These frogs frequent the swamps of the Swan coastal plain which are dry in summer. During the summer drought the animals take refuge beneath fallen vegetation and in holes and cracks in the ground. They are not capable of excavating holes for themselves.

Biology

Voice.—The *Chv* race has a harsh squelching call while the *Cc* race is a high-pitched “cheep”, “cheep”. This species commences to call after rain in April before swamps are full. Air temperatures at which males call range from 18 to 5.7°C. Clasping pairs are found after rain.

Life history.—Eggs are found singly or in clumps lying on the mud or attached to the debris at the bottom of water. At Attadale the number of eggs per female,

ignoring polymorphs, varies from 66 to 194. On Rottnest I. the maximum number recorded is 203 and at Gingin 268. The numbers for the *Cc* race varies from 117 to 249.

Egg dimensions varied as follows: *Chv* race, capsule diameter 1.76–2.10 mm, yolk diameter 1.11–1.46 mm; *Cc* race, capsule 1.69–1.92 mm and yolk 1.09–1.27 mm in diameter respectively. These values represent ranges of means for various egg masses. Eggs kept at constant temperature of 16°C hatched in 9–10 days and at 22°C in 8 days.

At hatching, larvae are about 4.8 mm long. The *Chv* race of *insignifera* takes longer than 140–150 days to metamorphose at 16°C. At 22°C this time is shortened and ranges from 85 to 105 days; the *Cc* race takes longer than 142 days at 16°C, but the *Cc* race from Caversham takes less than 163 days.

Food.—These frogs appear to be non-specific predators and eat any small insect. The following have been recovered from faeces: wings of Diptera (Culicidae and Simuliidae), beetle elytra, ants (wings and heads of *Iridomyrmex*), Acarina (oribatids and red-legged earth mites), legs of Acrididae; Collembola (sminthurid); and shells of the snail *Luinodiscus*.

CRINIA PSEUDINSIGNIFERA, sp. nov.

Crinia signifera in part, Main, 1954, op. cit. p. 123.

Diagnosis.—Morphologically similar to other members of the *insignifera* super-species from which it is distinguished by male call and hybrid inviability as demonstrated by *in vitro* matings (Table 5). In the preceding Sections this species has been referred to as the *Phv* race. Size range is shown in Figure 5.

Type.—Male No. 1000/54 in the Zoology Department Collection, University of Western Australia.

Type locality.—Yorkrakine Rock, 15 miles north of Tammin.

Specimens examined.—Nebree Spring, 2 ♂♂, 1 ♀; Koodiwoodie, 10 ♂♂, 6 ♀♀; Dongara, 7 ♂♂; Chittering, various sites, 4 ♂♂, 3 ♀♀; Bullbrook, 3 ♂♂; Red Hill, 2 ♂♂, 1 ♀; Walyunga, 3 ♂♂; Helena Valley, 5 ♂♂, 3 ♀♀; Mundaring, 5 ♂♂; Darlington, 2 ♂♂, 1 ♀; Boya Quarry, 15 ♂♂, 7 ♀♀; Beechina, 33 ♂♂, 9 ♀♀; Clackline, 1 ♂; Northam, 1 ♀; Quairading, 7 ♂♂; Waeel, 1 ♂; Yorkrakine Rock, 16 ♂♂, 6 ♀♀; Moorine Rock, 3 ♂♂; Kwolyin, 18 ♂♂; Albany Rd., 217 mile-post, 3 ♀♀; Lake Muir, 2 ♂♂, 3 ♀♀; Yallingup turnoff, Dunsborough, 1 ♀; Augusta–Nannup Rd., 8 ♂♂, 7 ♀♀; Stirling Ranges, 11 ♂♂, 4 ♀♀; Jarramongup, 8 miles east of, 1 ♂, 1 ♀; Peak Charles, 2 ♂♂; Doubtful Island Bay, 1 ♀; Ravensthorpe, 18 miles west of, 3 ♂♂, 2 ♀♀; Ravensthorpe, 5 miles east of, 1 ♂; Junana Rock and Pine Hill, 2 ♂♂, 3 ♀♀; Esperance, Dempster's Head, 4 ♂♂.

Range.—Reaches the west coast between the Moore R. and Dongara. South of the Moore R. it is restricted to the plateau east of the Darling Range. The northern and eastern boundary is a line joining Dongara, Mingenew, Gunyidi, Yorkrakine Rock, Moorine Rock, Peak Charles, and Pine Hill.

Habitat.—Restricted to summer-dry swamps, which on the Western Australian plateau are of local extent being generally associated with the run-off from large granite hills which are a characteristic feature of the plateau. These habitats are commoner along the western and southern boundaries of the range.

Biology

Voice.—A rather high-pitched, wavering "baa", "baa", "baa", . . . repeated. Males have been heard calling in air temperatures ranging from 18 to 6.5°C. On July 16, 1954, clasping pairs were seen at Beechina. At this time no eggs or larvae of *Crinia* were present so presumably no eggs were laid prior to this date. Calling males and clasping pairs may be found out of water.

Life history.—The egg numbers per female at Beechina range from 77 to 135 while one specimen from Doubtful Island Bay gave 207. Egg dimensions varied as follows: capsule 1.72–2.53 mm, yolk 1.21–1.46 mm in diameter, these values representing ranges of means of various egg masses. Eggs kept at 16°C hatched in from 11 to 13 days. These times are a little longer than those taken by *insignifera* under the same temperature conditions. It seems likely that *pseudinsignifera* larvae are subject to a greater daily range of temperature as well as a higher daily maximum than *insignifera* larvae. This is brought about by the reduced cloudiness on the plateau which allows for a greater heating of water by insolation during daylight and a more intense cooling with clear skies at night.

At hatching larvae range from 5.1 to 6.6 mm for different egg masses. Specimens 5.1 mm long had a body of 1.75 mm. At 16°C larvae take 148–157 days to metamorphose. Time from egg to metamorphosis in the field may be as short as 82 days or as long as 102 days at Beechina. For the Stirling Ranges specimens, larval life may be as long as 130 days.

Larvae have the general appearance as in Figure 2(h). They are decidedly more mottled and distinctly lighter in colour than *glauerti* larvae. The larvae of *insignifera* and *pseudinsignifera* cannot be distinguished, the larva figured (from Beechina) was 21.5 mm long of which 8.0 mm was body which was 5.0 mm deep. Spiraculum not visible from above, tail long and bluntly rounded with many guanophores. Ventrally the spiraculum is on a small mount. Papillae may be in corner of mouth or across lower lip. Lip-teeth variable, either a $\frac{1}{2}-\frac{1}{1}$ or a $\frac{1}{3}-\frac{1}{1}$ formula in which latter case the third lower row is short and situated medially. Anus opens to the right on a very short tube. At Beechina, larvae were seen to congregate in sunlit, shallow water where the temperature was 25°C. Juveniles which have just completed metamorphosis measure from 7.6 to 9.6 mm.

Food.—The following have been found in faeces: beetle elytra; wings of Diptera, heads of ants (*Camponotus*), shells of *Luinodiscus*.

CRINIA PARINSIGNIFERA, sp. nov.

Diagnosis.—Male: throat dark, colour more extensive than *insignifera*, white pectoral spots, belly evenly dark grey. Voice like *insignifera*. Female: belly dirty white or finely flecked with small grey spots. Throat dark grey. The polymorphs characteristic of all the rough-bellied species of *Crinia* are found. Size range of Kingston-on-Murray specimens are shown in Figure 5.

Males may be distinguished from *signifera* and *glauerti* and *pseudinsignifera* males by their call. Morphological features such as vomerine teeth give no assistance

in distinguishing these species. Females can be distinguished from *signifera* and *glauerti* females by the absence of mottling on the belly. There appears to be no consistent morphological feature which will separate females of this species and the other species of the *insignifera* super-species. Marked hybrid inviability occurs when crossed with species of the *signifera* and *insignifera* super-species.

Type.—Male No. 431/55 in the Zoology Department Collection, University of Western Australia.

Type locality.—Kingston-on-Murray, S.A.

Specimens examined.—Blanchetown, S.A., 1 ♂; Kingston-on-Murray, S.A., 14 ♂♂, 1 ♀; Horsham, Vic., 7 miles north of, 8 ♂♂, 1 ♀.

Range.—This species has been heard calling in daylight at Renmark, S.A., Lake Cullalleraine, Vic. (37 miles west of Mildura), and at Warracknabeal, Vic. Not found or heard calling south of Horsham, Vic., or at Murray Bridge, S.A., presumably restricted to the Murray Valley, up stream from Murray Bridge, and the Wimmera district of Victoria. Probably occurs also in the Darling River system.

Habitat.—At Blanchetown and at Kingston-on-Murray, frogs were calling from a shallow flooded area on river alluvium where dead sticks of a summer-growing composite and dead grass stalks indicated that it was a summer-dry swamp which had been flooded and filled by recent rains. Reeds and other aquatic vegetation characteristic of permanent water were absent.

Biology

Voice.—Extremely similar to that of *insignifera* (it may be likened to the noise produced by drawing a wet finger over an inflated rubber balloon). At Renmark, males of this species were calling on August 14, 1955, in bright sunlight at 11.30 a.m. with water temperature 13°C and air temperature 23°C; 7 miles north of Horsham males were calling at 8 p.m. with air and water temperatures 9 and 8°C respectively.

Life history.—No larvae of *Crinia* species were seen at any of the sites where adults of this species were collected. Breeding is probably associated with the annual flooding of the billabongs along the Murray R., or other suitable places throughout the drier country inland from the Great Dividing Range.

KEY TO WESTERN AUSTRALIAN SPECIES OF THE GENUS CRINIA*

1. Ventral surface smooth 2
- Ventral surface granular 3
- 2(1). Throat of male dark, belly of male and female pink *rosea* Harrison
- Throat and belly of males and females yellow-brown or brown, no red colouring *leai* Fletcher
- 3(1). Large species, 18–38 mm long, hind surface of thigh and groin bright red, throat of male dark, with white pectoral spots, belly of male dirty white or grey, throat and belly of female white *georgiana* Tschudi
- Small species, 14–24 mm long, lacking red on thighs and groin 4
- 4(3). Throat of breeding male dark, with white pectoral spots; belly of females boldly marked in black and white (*signifera* super-species) 5

* *C. parinsignifera*, sp. nov. and *C. signifera* from eastern Australia also included.

Throat of breeding male white or grey, chin only dark, white pectoral spots absent or inconspicuous; belly of females white or only speckled with black, never boldly marked (*insignifera* super-species) 6

5(4). Mature males about 20 mm long, belly and hind legs mottled in black and white. Females about 23 mm long, belly and hind legs mottled in black and white *signifera* Girard

Mature males small, about 15 mm long, belly very dark, usually only a few small white spots, hind legs never mottled. Females 16–18 mm long, belly and hind limbs boldly mottled in black and white *glauerti* Loveridge

6(4). Males with belly white, throat grey, and chin dark. Females with belly and throat white, lightly flecked on leg.

W.A. *insignifera* Moore

Murray Valley, east. Aust. *parinsignifera*, sp. nov.

Males with belly flecked with black, throat grey, chin black. Females with throat and belly heavily flecked in black. W.A. *pseudinsignifera*, sp. nov.

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Lastly, it is desired to thank Dr. J. A. Moore for comparing photographs of *C. insignifera*, race *Chv*, with the type and paratype of *C. insignifera* and for comparing these with paratypes of *C. glauerti*.

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A CYTOTAXONOMIC STUDY OF THE *PUSILLA* GROUP OF SPECIES IN THE GENUS *AUSTROICETES* UV. (ORTHOPTERA: ACRIDIDAE)

By M. J. D. WHITE* and K. H. L. KEY†

[Manuscript received August 7, 1956]

Summary

Cytological study of the members of the *pusilla* group has shown that the "inland race" of *A. pusilla* (Walk.) differs in several constant chromosomal features from the other races and must be regarded as a distinct species; this has been described as *A. interioris*, sp. nov. The alleged "intergradation" between the two forms is to be ascribed to overlap in phenotypic characters and not to interbreeding, the "intermediates" being always cytologically typical of one or other species. Certain phenotypic characters are fully diagnostic when present, but a small proportion of individuals in eastern Australia and a much larger proportion in South Australia and Western Australia cannot be determined with certainty on the phenotype. *A. nullarborensis* Key differs cytologically from both the other species.

The taxonomy and distribution of the three species is discussed. *A. pusilla* and *A. interioris* cannot be regarded as species *in statu nascendi*, and their interrelations induce scepticism in regard to claims to have recognized introgressive hybridization in various groups of animals by classical taxonomic methods. The bearing of the new information on the phylogeny of the group is indicated.

I. INTRODUCTION

The taxonomy, variation, and distribution of the Australian grasshopper genus *Austroicetes* have been dealt with by Key (1954). However, subsequent cytological analysis of some of the members of this genus has thrown new light on their status. The results provide a striking example of the application of cytological methods to a difficult taxonomic problem. What appeared to be a *Rassenkreis* with a high degree of reproductive isolation between its terminal members (where the ranges of these overlap) is here shown to consist of two entirely distinct species. And a situation that was extremely suggestive of introgressive hybridization now appears to be due to convergent evolution in the same habitat, or to the retention in both forms of the same ancestral genetic potentiality for clinal variation.

Of the eight species of *Austroicetes* previously recognized, we are here concerned with the closely related pair *A. pusilla* (Walk.) and *A. nullarborensis* Key. Both exhibit a number of distinct colour patterns, presumably due to genic polymorphism, which formed the basis for Key's "homologous varieties". We prefer to call these "pattern morphs", after Huxley (1955).‡ In addition, *nullarborensis*

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‡ The term "variety" has fallen into disrepute in zoology because of its ambiguity. And although these forms may be severally homologous as between species, they are not homologous one with another within a species, so that the use of "homologous" as an unqualified epithet is confusing.

(but not *pusilla*) shows kentromorphic phase differences (see Key and Day 1954, p. 322, footnote) in coloration and bodily proportions; and *pusilla* (but not *nullarborensis*) shows marked geographic variation.

Key (1954) described four "forms" (designated 1-4) of *pusilla*, each of which was predominant in a different geographic region, although also present elsewhere. The populations of these regions were designated "races" as follows: (a) a south-eastern race in south-eastern New South Wales, almost the whole of Victoria, Tasmania, and the higher-rainfall areas of South Australia as far west as Spencer's Gulf; (b) a north-eastern race in south-eastern Queensland and north-eastern New South Wales; (c) a south-western race in Eyre's Peninsula and some areas of Western Australia; (d) an inland race in the more arid regions of western New South Wales and South Australia and around the fringes of the Nullarbor Plain.

Extensive intergradation and overlap between forms 1, 2, and 3 occurs over wide areas and the races based upon them are clearly contained within the limits of a single species. The situation with regard to form 4 is different, however. Key stated that "there seems to be extraordinarily little overlapping between the range of form (4) [i.e. that typical of the inland race] and the ranges of the north-eastern and south-eastern races. Further, where overlapping does occur, intermediates are extremely rare . . . Thus if one were to rely upon the evidence from eastern Australia alone, it would be necessary to regard form (4) as constituting a distinct subspecies with a high degree of reproductive isolation. However, . . . on Eyre's Peninsula there is both overlap and extensive intergradation between form (4) and form (3), and the same is true of Western Australia . . .".

Sharman (1952) briefly described the chromosomes of the south-eastern race of *pusilla* from Tasmanian material, reporting that $2n\delta = 23$, all the chromosomes being acrocentric except for a medium-sized metacentric pair, in which a pericentric rearrangement had presumably reached fixation.

II. CYTOLOGICAL OBSERVATIONS

Testicular material of what we may still for the moment call "*pusilla*" was obtained from the following sources:

State	No. of Localities	No. of Specimens
New South Wales (with A.C.T.)	14	43
Victoria	1	2
South Australia	25	79
Western Australia	1	7
	41	131

A single testis of *nullarborensis* was also studied. The localities from which these specimens came are shown by special symbols in Figure 6 and by bold-face type in the lists on pp. 75-77 and 80-81. The cytological material was fixed in Navashin's fluid, sectioned at 24μ , and stained in gentian violet by Newton's method.

(a) New South Wales and Victorian Material

Individuals of the south-eastern race of *pusilla* from Canberra were found to agree cytologically in all respects with Sharman's description. On the contrary,

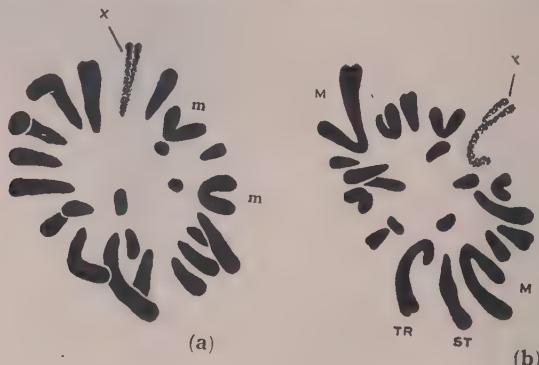


Fig. 1.—Spermatogonial metaphases: (a) *A. pusilla* (28 miles SW. of Whyalla, S.A.); (b) *A. interioris* (11 miles SE. of Port Augusta, S.A.). *m*, the small metacentric pair of *pusilla*; *M*, the large metacentric pair of *interioris*. This individual of *interioris* (the same as that shown in Fig. 3 (f)) had a medium-sized and a small pair of metacentrics, and a large pair (*ST* and *TR*) heterozygous for the "Trangie" rearrangement. Note the difference in the shape of the *X*-chromosomes of the two species.

material of form 4 from Fowler's Gap, north of Broken Hill, differed from this in a number of respects (Figs. 1-3) which, as confirmed and amplified from other material, may be tabulated thus:

Form 4

$$2n\delta = 21$$

A large metacentric chromosome, which has clearly arisen by a fusion, is invariably present in the homozygous condition

X-chromosome J-shaped, the short arm about 1/8 the length of the long arm

Smallest chromosome only slightly shorter than the next larger in the set

Chiasma frequency per nucleus = c. 12.5

A strong tendency to distal localization of chiasmata

All populations apparently contain several pericentric rearrangements and most individuals are structurally heterozygous

South-eastern Race

$$2n\delta = 23$$

No large metacentric; instead there is a medium-sized metacentric element, likewise invariably homozygous, which has presumably arisen by pericentric inversion

X-chromosome strictly acrocentric, its short arm minute and ordinarily invisible

Smallest chromosome much shorter than the next larger in the set

Chiasma frequency = c. 16.7

Many chiasmata interstitial; localization not evident

No structural polymorphism

These are very considerable differences, which would seem to render interbreeding most unlikely. In particular, the last three points suggest that the two forms have quite different genetic systems. Thus it appeared probable that "form 4" was an entirely distinct species.

Fowler's Gap and Canberra are well within the areas occupied exclusively by form 4, on the one hand, and by the south-eastern race on the other. Further material of form 4 from 9 miles W. of Weethalle, N.S.W., and of the south-eastern race from 5 miles W. of Murchison, Vic. (localities also within the areas of "exclusive occupation" but more peripherally situated within them) confirmed the cytological differences tabulated above. The remaining New South Wales material came from the region of overlap in the distributions of form 4 and forms 1-3, i.e. from near the boundary between the territory of the "inland race" and that of the south-eastern race (including in the latter, for convenience in the discussion, populations intermediate between the south-eastern and north-eastern races).

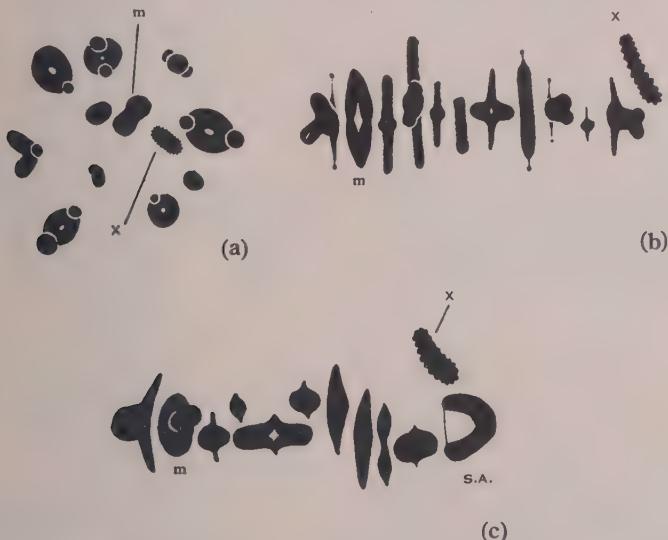


Fig. 2.—*A. pusilla*: (a) first metaphase in polar view (17 chiasmata present); (b) in side view (both (a) and (b) from 9 miles NNE. of Marsden, N.S.W.); (c) first metaphase in side view (Canberra, A.C.T.). *m*, the medium-sized metacentric bivalent; *S.A.*, a bivalent with a chiasma in the short arm. Note the short arms on the ends of several of the bivalents in (b).

Out of 11 series of specimens from the region of overlap, that from 16 miles ENE. of West Wyalong (one specimen) represented form 2. The series from 4 miles ENE. and 11 miles NW. of West Wyalong, 3 miles NW., 13 miles SSE., and 15 miles E. of Condobolin, and 7 miles E. of Ungarie (15 specimens in all) belonged to form 4. In three series (two specimens from 25 miles SW. of Forbes; five from Trangie; and 10 from Myall Mundi Station, 4 miles NW. of Trangie) form 4 was present together with forms 1 and 2 and intermediates between the latter, and the Myall Mundi series also included one specimen classed as intermediate between form 4 and form 1 or 2. A series from 9 miles NNE. of Marsden included three specimens referable to form 1 or 2 and two classed as intermediate between these and form 4.

At Myall Mundi a fairly dense population of forms 1-2 occurred in an area where the soil was of the grey "self-mulching" type (see Key 1945) and the habitat

was of type 2 (c) or 2 (f) (ii) of Clark (1949). About 50 yd away, on bare areas of red-brown sandy loam (Clark's habitat 2 (f) (i)), a population of form 4 was found. There was virtually no admixture, i.e. only two individuals of form 4 were found on

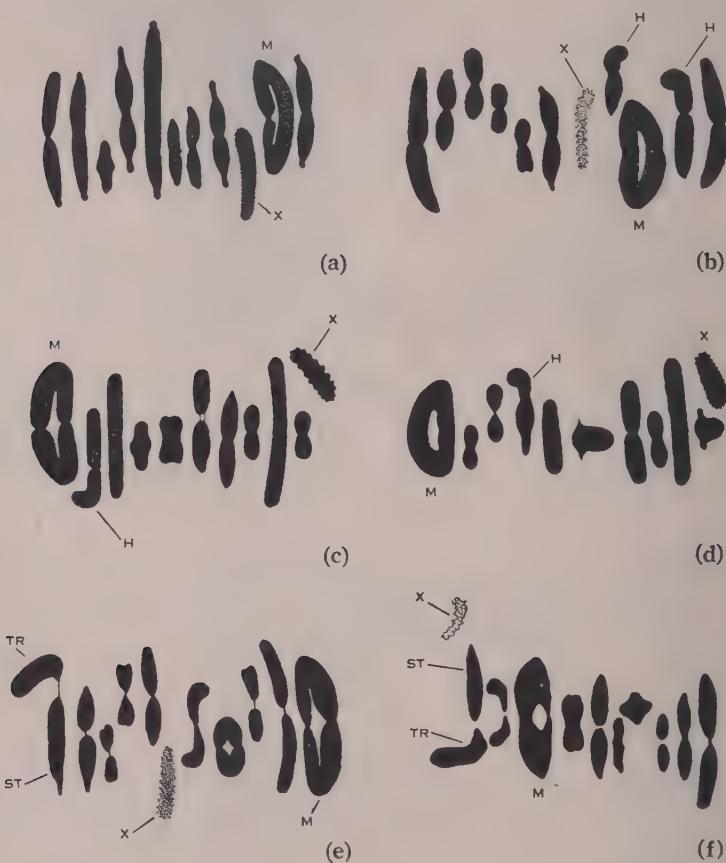


Fig. 3.—*A. interioris*, first metaphases of six individuals, in side view: (a) from 2 miles W. of West Wyalong, N.S.W.; (b) from 4 miles ENE. of West Wyalong, N.S.W.; (c) from 9 miles W. of Weethalle, N.S.W.; (d) from Fowler's Gap, N. of Broken Hill, N.S.W.; (e) from Myall Mundi Sta., 5 miles NW. of Trangie, N.S.W.; (f) from 11 miles SE. of Port Augusta, S.A. *M*, the large metacentric bivalent, which always has two chiasmata, one in each arm; *H*, the bivalents heterozygous for pericentric rearrangements; *ST* and *TR*, the "Standard" and "Trangie" arrangements of one of the long chromosome pairs (individuals (a), (b), (c), (d) were homozygous for the Standard sequence of this chromosome).

the grey soil and none of forms 1–2 on the red soil. The individual of intermediate phenotype was collected on grey soil. These findings agree with Key's (1954) account of the soil preferences of the two forms in the region of overlap and have been confirmed by Mr. L. J. Chinnick (personal communication) at the same spot.

Cytological study of this material from the region of overlap showed that all the differences previously noted between form 4 and the remaining forms of "pusilla" were present. The "intermediates" were cytologically indistinguishable from the south-eastern race. A single specimen from the Wyalong-Forbes region (precise locality not recorded) was classed as intermediate on external phenotype, but proved to be cytologically identical with form 4. In addition to two pericentric rearrangements also found in the material of form 4 from 9 miles W. of Weethalle, a very striking rearrangement was found in the heterozygous condition in several individuals of form 4 from Trangie and Myall Mundi. Bivalents heterozygous for this "Trangie" rearrangement (Fig. 3) are L-shaped at first metaphase, consisting of an acrocentric and a J-shaped element lying with its long limb in a "horizontal" plane. The latter element has presumably undergone a very long pericentric inversion.

Thus the cytological evidence from central New South Wales also suggests that form 4 is an entirely distinct species from *pusilla* and that the supposed intermediates are not such, but simply individuals of one of these species showing some of the characters ordinarily diagnostic of the other. The cytological evidence excludes the possibility that these anomalous individuals have originated by introgressive hybridization and lends no support to the view that introgression might have occurred in the past.

(b) *South Australian Material*

Material of "pusilla" was obtained from 25 localities in South Australia (Table 1), including five in Eyre's Peninsula where, according to Key (1954), extensive intergradation occurs between forms 3 and 4. Several other localities are near Key's tentative boundary between the south-eastern and inland races in the south-eastern part of the State, where overlap and perhaps intergradation of forms 1-3 and form 4 might be expected. The material was classified by Key's criteria into forms 1-3, form 4, and intermediate. There were 12 series comprising only forms 1-3, five comprising only form 4, two in which both were present, and seven (including three from Eyre's Peninsula) in which "intermediates" occurred.

Cytologically, all individuals classified as forms 1-3, all the 13 "intermediate" individuals, and five specimens (from four different localities) classified as form 4 were indistinguishable from the material of forms 1-3 from New South Wales and Victoria and had none of the chromosomal characteristics of form 4. On the other hand, 11 individuals (from three localities near Nackara and Port Augusta) classified on external phenotype as form 4 were cytologically similar to form 4 from New South Wales, although the short arm of the X-chromosome was possibly somewhat longer. Several of these individuals were heterozygous for the Trangie rearrangement.

Thus the two species with these very different karyotypes remain just as distinct in South Australia as in New South Wales, but the overlap in phenotypic characters is much wider, so that the proportion of "intermediates" is higher and misidentifications of forms 1-3 as form 4 occur.

A single individual of *A. nullarboensis* was studied cytologically (Fig. 4). It was collected at Nackara, in an area where cytologically authenticated individuals of both forms 1-3 and form 4 also occur. This individual had $2n\delta = 21$. A fusion

between two large chromosomes has given rise to a metacentric similar to the one constantly present in form 4; but the metacentric bivalent of *nullarborensis* shows 3-4 interstitial chiasmata, which give it an entirely different appearance from that of form 4, which invariably shows only one chiasma in each arm, terminalized by metaphase. In fact, in the frequency and distribution of its chiasmata, *nullarborensis* resembles forms 1-3 of *pusilla* rather than form 4.

TABLE 1
SPECIMENS OF AUSTRALOCETES "PUSILLA" FROM SOUTH AUSTRALIA, CLASSIFIED ON
EXTERNAL PHENOTYPE AS FORMS 1-3, FORM 4, AND INTERMEDIATE

Locality	Forms 1-3	Form 4	Intermediate
1 mile S. of Black Springs	—	—	1
5 miles SSW. of Callington	2	—	—
2 miles W. of Eudunda	8	—	—
12 miles E. of Eudunda	—	1	—
6 miles N. of Goolwa	1	—	—
Lake Hamilton (S. end)	1	—	—
5 miles N. of Laura	2	—	2
1 mile WSW. of Morgan	1	1	—
Nackara	1	—	—
10 miles SW. of Nackara	1	—	1
2 miles SW. of Normanville	2	—	—
4 miles NW. of North Shields	4	—	3
6 miles SE. of Orroroo	1	—	—
6 miles WNW. of Orroroo	5	—	—
17 miles SW. of Port Augusta	1	—	—
4 miles NW. of Port Wakefield	5	—	—
3 miles SW. of Tailem Bend	4	1	4
3 miles NW. of Tailem Bend	—	2	—
6 miles NE. of Tumby Bay	1	—	1
2 miles NW. of Two Wells	5	—	—
28 miles SW. of Whyalla	4	—	1
1 mile S. of Wirrabara	1	—	—
4 miles SW. of Nackara	—	1	—
11 miles SE. of Port Augusta	—	1	—
13 miles SE. of Port Augusta	—	9	—

The individual of *nullarborensis* examined was also homozygous for two other metacentrics, one medium-sized (Fig. 4, *m*) and one small. The former could be the same element as the similar-shaped chromosome of forms 1-3 of *pusilla*, but the identity is not certain. The *X* of *nullarborensis* is a metacentric with one limb about 2/3 the length of the other, so that its shape is quite different from that of the other members of the *pusilla* group. One cannot tell, from a single, cytologically homozygous individual, whether populations of *nullarborensis* show any cytological polymorphism or not.

(c) Western Australian Material

Of seven individuals of "pusilla" from 1 mile W. of Edah (Mt. Magnet area), six were classified on external phenotype as form 3, or intermediate between forms 3 and 1, although several could almost as well have been regarded as intermediate between forms 3 and 4. The remaining one was classified as form 4, although not differing greatly from the others. Cytologically all seven were indistinguishable from material of the south-eastern race from New South Wales.

Thus the situation in Western Australia is probably similar to that in South Australia, with some individuals of the south-western race exhibiting phenotypic characters previously regarded as diagnostic for form 4.

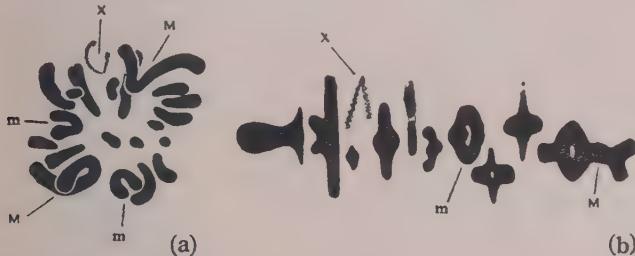


Fig. 4.—*A. nullaborensis* (Nackara, S.A.): (a) spermatogonial metaphase in polar view; (b) first metaphase in side view. *M*, the large metacentric pair; *m*, the medium-sized metacentric pair. In (b) the *M* bivalent has four chiasmata. Note the metacentric form of the *X*. The smallest chromosome pair is comparable in size with that of *pusilla* (cf. that of *interioris*).

(d) Conclusions

The cytological evidence demonstrates that:

- (i) Form 4 of "pusilla" constitutes an entirely distinct species, which could not be expected to interbreed with forms 1-3.
- (ii) Forms 1-3 are cytologically indistinguishable throughout their range, so that their conspecificity is supported by their cytology.
- (iii) The supposed intermediates between form 4 and forms 1-3 are due to overlap in the ranges of their phenotypes and not to hybridization.
- (iv) The distinctness of *nullaborensis* from the other two species, in spite of rather slight phenotypic differences from form 3, is confirmed.

III. TAXONOMY

We have examined the holotype of *A. pusilla*, which is a typical specimen of form 1. Since only cytological criteria are decisive for separating the two species hitherto confused under the name *pusilla* and the cytology of the holotype will never be determinable, we propose that the latter should be regarded as a member of the population having the karyotype described under "South-eastern Race" on p. 58, and that the type locality ("Australia") should be restricted to "Goulburn, N.S.W." *Chortoicetes pusillulus* Rehn, recorded as a junior synonym of *A. pusilla* (see Key 1954), seems from the description of the holotype to be more probably based on form 1

or 3 than on form 2 or 4; information kindly supplied by Mr. John C. Pallister, who at our request examined the holotype in the American Museum of Natural History, suggests that it is in fact intermediate between forms 1 and 3. This conclusion is consistent with the type locality ("Victoria"), since form 4 is known only from the north-west corner of that State. The female holotypes (examined by us) of the other two recorded synonyms of *pusilla*, *Chortoicetes vicina* Sjöst. and its "f. *plana*" Sjöst., must also be referred to forms 1-3 and this is consistent with their locality of collection (Canberra).

Thus all the nomenclaturally available names in the *pusilla* group seem to be excluded from applicability to the species formerly designated as form 4 of *pusilla*, or the "inland race". On p. 68 this species is described as *A. interioris*, sp. nov.

We have seen that the range of variation of *pusilla* and *interioris* overlaps with respect to all the phenotypic characters of value in determining them. Phenotypic "intermediates" are found and even misidentifications are possible. We have examined the internal genitalia of both species and also of *nullarborensis*, although these are seldom useful at the species level in this subfamily of Acrididae. Considerable intraspecific variation was noted in the structure of both epiphallus and phallus, with a suggestion of statistical interspecific differences, but nothing more diagnostic than the external characters.

The criteria given by Key (1954) for separating "form 4" from the other forms of his "*pusilla*" are of unequal diagnostic value. All the structural characters, for example, represent only trends, or statistical differences. The only characters which, at least formally, permitted definite determinations were the following:

Form 4

Internomedian area of hind femur with the bands dark, sharply demarcated and uninterrupted, the medial band less than twice the width of the area proximal to it

Ventrointernal area of hind femur with the distal band present
Hind tibia of male partly red in some individuals

Forms 1-3

Internomedian area with the bands dark, sharply demarcated and uninterrupted, but the medial band of the male at least twice the width of the proximal area (forms 1 and 2); or the bands less dark, more or less interrupted or incomplete, the medial band less than twice the width of the pale proximal area (form 3)

Ventrointernal area with distal band absent (forms 1 and 3), or present (form 2)
Hind tibia of male never red

Of these, the last two enable some, but by no means all, individuals to be determined. The following uncertainties may arise in the application of the first two: (1) whether the bands on the internomedian area should be classed as dark or not and as interrupted or not; (2) whether a very narrow or faint proximal extension of the medial band should be counted when estimating the width of this band; (3) whether a very faint infuscation on the ventrointernal area should be counted as a band.

The characters listed were used to determine the form to which each of the males studied cytologically belonged, all other characters being disregarded for this

purpose. Specimens classed as intermediate either had individual characters in a borderline condition, as indicated in (1) to (3) above; or they exhibited characters of both form 4 and forms 1-3 in one or other of the following possible combinations: (a) internomedian area as in forms 1-3, hind tibia red; (b) internomedian area as in form 4, ventrointernal area with the distal band absent.

We have seen that in six of the 131 males of *pusilla* and *interioris* studied cytologically the application of the above phenotypic criteria had led to the misidentification of *pusilla* as *interioris*. Five of these were from the region of South Australia where form 1 is dominant and these may be interpreted as intermediates between form 1 and form 3, the medial band of the internomedian area being narrower than typical for form 1, but not yet interrupted as in typical form 3. The sixth was from Western Australia. In four of the misidentified specimens the medial band was narrow and uninterrupted and the distal band on the ventrointernal area present. The remaining two were similar, but the medial band extended a little proximal of the critical point (i.e. the point where this band becomes twice as wide as the proximal pale area) as a faint suffusion. It is of interest that, when a subjective assessment on the basis of the totality of their characters was made, four of the specimens were classed as nearer *pusilla* and only two as nearer *interioris*.

Of the 17 phenotypically intermediate males studied cytologically, one was *interioris* and 16 *pusilla*. The one *interioris* (from New South Wales) had the medial band of the internomedian area extending almost to the base of the area and the hind tibia red. It was therefore a most striking example of phenotypic intermediacy. Of the 16 *pusilla*, 13 were from South Australia (Eyre's Peninsula and east of Spencer's Gulf). These showed various types of intermediacy in which the internomedian area was as in form 4 or deviated only slightly from that condition, while the distal band on the ventrointernal area was absent or very weak. On general appearance, 11 were classed as nearer *pusilla*, one as nearer *interioris*, and one as indefinite. The remaining three *pusilla* with an intermediate phenotype were from New South Wales. Two of them were teneral and the intermediacy probably spurious, and the third had the medial band slightly interrupted and extending proximal of the critical point as a suffusion.

Thus it appears that the phenotypic criteria employed favour *interioris*, in that many specimens of *pusilla* were classed as *interioris* or intermediate, while only one *interioris* was classed as intermediate and none as *pusilla*. However, any shift of the dividing line towards *interioris* would immediately result in some specimens of that species being misidentified, so that phenotypic overlap is inescapable. Determinations based on "general appearance" (i.e. an integrated subjective assessment of all characters, including those representing only trends with many exceptions or wide overlap) may seem more reliable than those based on objective use of a few critical characters. Unfortunately, one cannot maintain constant standards in such subjective determinations, conflicting judgments on the same material being given at different times.

Although it is not possible to make a positive identification of every specimen on the phenotype, the evidence suggests that certain phenotypic characters, when

present, are completely diagnostic. These "fully diagnostic phenotypic criteria" are as follows:

<i>interioris</i>	<i>pusilla</i>
Hind tibia pink to red in male	
	Internomedian area of hind femur with the medial band extending to the base of the area; or internomedian area with the bands markedly interrupted and pale, ventrointernal area with the distal band absent

As a further safeguard, it would be advisable to require that identifications by these criteria should be consistent with the indications of the less restricted criteria previously employed (those tabulated on p. 64) and, in the case of *pusilla* from South Australia, that they should not be contradicted by the "general appearance".

There are thus the following three categories of determination, in descending order of reliability and differing in applicability:

- (i) Based on cytology. (Entirely reliable. Applicable to *living* individuals of both sexes and all stages.)
- (ii) Based on "fully diagnostic phenotypic criteria". (Believed to be entirely reliable or almost so. Applicable to about half the adult males of *interioris*, but not to its females; to almost all adults of the north-eastern race of *pusilla*; to a rather small proportion of the adult males, and a still smaller proportion of the females, of the south-eastern race; and to a small proportion of the adults of the south-western race.)
- (iii) Based on other phenotypic criteria. (Unreliable in a proportion of cases ranging from a very low percentage in New South Wales to perhaps 10–20 per cent. in parts of South Australia and Western Australia. Applicable to all adults.)

The reliability of determinations in category (iii) can be increased by taking account of the locality. Thus a condition of the bands of the internomedian and ventrointernal areas immediately diagnostic of *interioris* in New South Wales would need to be much more carefully considered in material from South Australia or Western Australia, where *pusilla* approaches closer to *interioris* in its phenotype. In these regions a specimen needs to be determined as *pusilla* unless it is in every respect typical of *interioris*.

All available material of *pusilla* and *interioris*, comprising almost all that available to Key in 1954 together with collections made since, has been re-examined and determined by these criteria. Many specimens with intermediate characters and combinations of characters have been noted, adding considerably to the number and variety of phenotypic intermediates hitherto noted. The more interesting are reviewed below.

(a) Material from New South Wales, Victoria, and Tasmania

Determined as *interioris*:

- (1) A female from Goombalie and a male from Birkalla, N.S.W., resemble a male already discussed in having the medial band on the internomedian area

reaching the base of the area although somewhat narrowed and interrupted in the proximal portion and the distal band present on the ventrointernal area.

(2) A female from near Barnato Tank, N.S.W., lacks the distal band from the ventrointernal area. The condition of the medial band on the internomedian area is not determinable, the area being discoloured.

(3) Males from Broken Hill and near Packsaddle Tank and females from near Grenfell and Grong Grong, N.S.W., have the medial band, or both bands, of the internomedian area markedly interrupted, but the distal band present on the ventrointernal area.

Determined as *pusilla*:

(4) Females from Boggabri, Jerry's Plains, and near Singleton, N.S.W., have the medial band reaching or nearly reaching the base of the internomedian area and the inner margin of the ventrointernal area distinctly pink. The latter is a character usually confined to *interioris* (see Key's description of "form 4", 1954). The distal band of the ventrointernal area may be present or absent.

(5) Males from the vicinities of Young, N.S.W., Dimboola, Vic., and Cleveland, Tas., have the medial band of the internomedian area uninterrupted and less than twice the width of the pale proximal area (except, in the first two localities, for a thin line extending more proximally), but the distal band absent from the ventrointernal area.

(b) Material from South Australia and Western Australia

Determined as *interioris*:

(6) A female from near Curnamona and one from 10 miles SW. of Tailem Bend, S.A., have the medial band of the internomedian area very slightly interrupted and the distal band on the ventrointernal area very dark but incomplete.

Determined as *pusilla*:

(7) Many specimens from South Australia and some from Western Australia are similar to those cited under (5) above.

(8) Material of both sexes from a number of localities in South Australia (vicinities of Eudunda, Lake Hamilton, Murray Bridge, Ceduna, Colonia, Eucla, and Tailem Bend) and Western Australia (vicinities of Kalgoorlie, Karonie, Madura, and Widgiemooltha) have the medial band of the internomedian area uninterrupted and less than twice the width of the proximal pale area, and the distal band of the ventrointernal area well developed. In some of these the medial band does not quite reach the ventral margin of the internomedian area.

(9) A female from Balladonia H.S. and one from near Norseman, W.A., have the bands of the internomedian area markedly interrupted and no distal band on the ventrointernal area, but the inner margin of the latter pink.

Thus the phenotypes that present the greatest difficulty in classification fall into three broad categories:

- i. Those in which *interioris* simulates the south-eastern and especially the north-eastern races of *pusilla* by showing a proximal extension of the

medial band of the internomedian area well beyond the critical point. This condition is uncommon and seems to be confined to New South Wales.

- (ii) Those in which *interioris* simulates the south-western race of *pusilla* in having the bands of the internomedian area interrupted, while retaining, at least partially, the distal band on the ventrointernal area. This condition also is uncommon, but occurs at several widely scattered localities in New South Wales and South Australia.
- (iii) Those in which *pusilla* simulates *interioris* by having the bands of the internomedian area uninterrupted and the medial one less than twice the width of the pale proximal area, the distal band on the ventrointernal area being absent or present. This condition is frequent and widespread in South Australia and Western Australia, but uncommon in Victoria and Tasmania and rare in New South Wales. It gives rise to special difficulty when the distal band on the ventrointernal area is well developed, for such phenotypes have the major hall-marks of *interioris*.

Thus the results of this re-examination of the material are in complete agreement, so far as the phenotype is concerned, with the conclusions reached by Key (1954). That is, in New South Wales and Victoria there is little evidence of intermediacy and almost all specimens are readily identifiable. On the contrary, in South Australia and Western Australia there is "extensive intergradation", and recognition of *interioris* on phenotypic characters becomes a matter of great difficulty. But for the cytological evidence, we should probably be led to taxonomic conclusions differing only slightly, if at all, from those of Key.

In the formal taxonomy that follows, portions of Key's treatment of *pusilla*, affected by his failure to distinguish the two species, are corrected and new information on that species and on *nullarborensis* added. The internal male genitalia have been examined in six specimens of each of the three species. The figures are based on what appear to be the most distinctive preparations in each species. It may be noted that *interioris* would key out as *pusilla* in the key to the species of *Austroicetes* presented by Key (1954). It would be practicable to separate the two species in a key only by using chromosomal characters.

AUSTROICETES INTERIORIS,* sp. nov.

Figs. 1(b), 3, 5(a), 6

Austroicetes pusilla, Key partim (nec Walk.), 1954 (form 4 and inland race), pp. 126–42, figs. 23, 25.

Holotype.—A male from 7 miles E. of Ungarie, N.S.W., 24. iii. 1956, L. J. Chinnick. ("M. J. D. White: cytol. prep. 1811".) *Allotype*.—A female from 3 miles NW. of Condobolin, N.S.W., 24. iii. 1956, L. J. Chinnick. *Paratypes*.—Males and females from many localities. The holotype and allotype and the slide showing the chromosomes of the holotype are in the Division of Entomology Museum, C.S.I.R.O., Canberra, along with numerous paratypes. Other paratypes have been deposited

* i.e. of the *interior*, suggesting its identity with the "inland race" of "*pusilla*" described by Key (1954).

in the Australian Museum, Sydney; the National Museum of Victoria, Melbourne; the South Australian Museum, Adelaide; the British Museum (Natural History), London; and the museum of the Academy of Natural Sciences of Philadelphia.

The material examined consists of 212 males, 177 females, and one juvenile. Of these, 150 males, 153 females, and the juvenile were included in the series examined by Key and bear his determination label "*Austroicetes pusilla* (Walk.)". One female is labelled as having been figured in Key's Figure 23; and four males and three females bear labels indicating that their measurements were published by Key (in his Table 20).

The points of resemblance and of difference between this species and *A. pusilla*, both phenotypic and chromosomal, have already been discussed in detail. From *nullarborensis* it differs in the same phenotypic characters as does *pusilla*, only more distinctly, there being none of the close phenotypic approximation found between *nullarborensis* and some individuals of the south-western race of *pusilla*. Thus *interioris* and *nullarborensis* may be visualized as diverging in opposite directions from *pusilla* in their phenotypic characters. While this is a convenient descriptive model, it does not necessarily reflect the phylogeny of the *pusilla* group. This question will be discussed further in Section V.

Morphology

Antenna very slightly flattened dorsoventrally in the proximal half, very slightly thicker in the distal half than in the proximal, with about 18-21 articles (many incompletely divided near distal and proximal ends); in the male longer, in the female varying from slightly shorter to slightly longer, than head and pronotum together. *Head* in profile strongly convex above, usually rising considerably above the level of the pronotum. Face slightly convex above the antennae, straight or very slightly convex below the antennae, slightly sloping to almost vertical. Fastigium strongly sloping, considerably impressed; anterolateral margins strongly incurved, often subparallel towards the apex, especially in the male; apex truncate or very occasionally rounded. Temporal foveole sharply pointed apically, open, partially closed, or (rarely) closed behind, dorsal margin somewhat convex or rarely straight, ventral margin straight or rarely slightly concave or convex; very rarely reaching apex of fastigium. An imaginary straight line from the apex of the fastigium to the dorsal margin of the lateral ocellus passes entirely ventral to the foveole or very rarely traverses its ventral margin. Frontal ridge sulcate for some way below the median ocellus, not right to the clypeus; above the ocellus sulcate, or rarely flat in part; margins gradually converging from clypeus to median ocellus, above the ocellus typically subparallel or even slightly diverging for a short distance and then converging again to the fastigium. *Pronotum* not, or little, wider posteriorly than the head, moderately constricted; in profile concave above, the concavity being due mainly to angulation at the third transverse sulcus or at both the third and first sulci; metazona convex or occasionally straight, rarely concave in part. Median carina usually intersected by the first transverse sulcus. Second sulcus usually well developed on the disk, usually continuous with the main part of the sulcus on the lateral lobes, often continuous to the median carina and sometimes intersecting

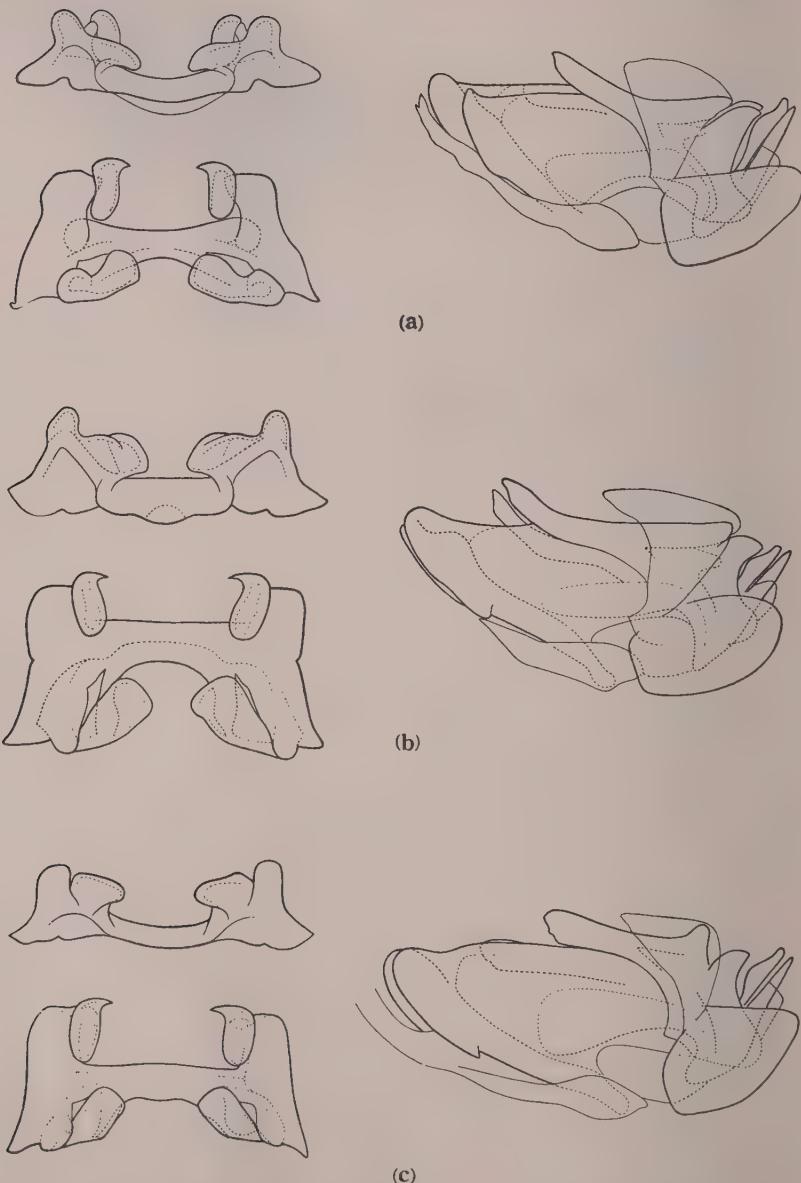


Fig. 5.—Epiphallus in dorsal and posterior views and phallus in left lateral view:
 (a) *A. interioris* (Myall Mundi, N.S.W.); (b) *A. pusilla* (Trangie, N.S.W.); (c) *A. nullaborensis* (3 miles WNW. of Penong, S.A., and 12 miles W. of Madura, W.A.).

it. Lateral carina nearly always discernible in both anterior and posterior portions, though poorly developed, especially in the latter. Posterior margin of pronotum

roundly obtusangulate, rarely almost evenly rounded. Metazona usually distinctly longer than prozona, very rarely subequal to it. Lateral lobe with the ventral margin somewhat ascending or rarely horizontal in the posterior half; posterior angle usually slightly more than 90°, rarely 90°. *Tegmen* exceeding the apex of the hind femur by a distance greater than, subequal to, or less than the length of the pronotum. *Hind femur* broad and thick, the dorsoexternal area at its widest point slightly to considerably more than half the width of the externomedian area at the same point; both inner and outer genicular lobes widely rounded. *Hind tibia* with 9–13 outer and 11–14 inner spines, usually 10 outer and 11 inner. *Hind tarsus* with the arolium small, oval, considerably longer than broad, $\frac{1}{3}$ – $\frac{1}{2}$ the length of a claw. *Abdominal terminalia* of male essentially as in *A. pusilla*, but the supra-anal plate with its posterior part usually somewhat longer relative to the anterior part and the lateral margins less raised.

Genitalia of male as in Figure 5(a), but variable in many points of detail. The differences between Figure 5(a) and the corresponding figures for *A. pusilla* and *A. nullarborensis* (Figs. 5(b) and 5(c)), while possibly representing definite trends, are not maintained consistently even within a sample of six individuals of each species. These include, in the epiphallus, the shape and size of the lophi and their inner lobes; the separation of the latter in relation to their width; and their orientation, whether predominantly mesad or dorsad. In the phallus they include the length of the apodemes relative to their separation, the relative lengths of the aedeagal valves and the dorsal portions of the rami, and the pointedness of the latter, as determined by the degree of convexity of their anterior margin in lateral view.

Cytology (Figs. 1(b) and 3)

$2n\delta = 21$. Homozygous for a large metacentric chromosome resulting from a fusion. This chromosome regularly shows two chiasmata at meiosis. Smallest chromosome only slightly shorter than the next larger. X-chromosome J-shaped, the short arm about 1/8 the length of the long arm. Chiasma frequency per nucleus= c. 12.5. A very strong tendency to distal localization of chiasmata. All or most populations polymorphic for several pericentric rearrangements; most individuals structurally heterozygous.

Coloration

Hind wing as in *A. pusilla*. *Hind femur*: Internomedian area straw-coloured, with the genicular, distal, and medial bands always present and nearly always very dark, sharply demarcated, and free from pale interruptions; the medial band nearly always less than twice the width of the pale proximal portion of the area and usually narrower than this portion, very rarely extending almost to the base of the area. Ventrointernal area straw-coloured, often with a reddish tinge on the extreme inner margin, especially in the female; the distal band almost always present and usually very strongly developed. Dorsoexternal area with the medial band triangular, its apex reaching the outer margin. *Hind tibia*: About the distal half pink to red in the female, in the male straw-coloured (often darkening to buff or light brown distally) or pink to red. About the proximal half straw to white;

TABLE 2
FREQUENCY OF THE DIFFERENT PATTERN MORPHS AND OF GREEN INDIVIDUALS IN ASTROCYTES INTERIORS

		Green												Total	
		<i>leopardina</i>						<i>porphyrica</i>							
		No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
Males	%	16	20	0	3	5	0	86	10	0	0	0	0	0	140
Females	%	17	31	0	0	11	0	62	11	0	0	0	0	1	11
		11.4	14.3	0	2.1	3.6	0	61.4	7.2	0	0	0	0	0	0
		11.8	21.5	0	0	7.6	0	43.1	7.6	0	0	0	0	0.7	7.6

black genicular band present on at least the inner face and almost always on the ventral face also. Distal band ranging from well developed to absent; best developed on the angle between the ventral and inner faces, but frequently strong on ventral, inner, and outer faces; very faint or absent on dorsal face. Sometimes there are scattered dark markings over much of the proximal half of the outer face. Abdomen usually a pale yellowish buff, sometimes darkening to brown above.

The dimorphism of the colour of the hind tibia in the male has been discussed by Key (1954, p. 136) under the "inland race" of "*A. pusilla*". He states that the two types of individual are about equally abundant east of the eastern border of South Australia and there is little indication of intermediate conditions, but that to the west of that line only the type with the straw-coloured tibia had been found. The material now available shows that both types occur in about equal numbers as far west (central South Australia) as the species is known with certainty to extend.

The following pattern morphs ("homologous varieties" of Key) are represented in the material: *trilineata*, *lineosa*, *anterolineata* (?), *nigrovirgata*, *rubiginosa*, *transmaculata*, and *porphyrica*. The record of *anterolineata* rests upon three somewhat doubtfully determined individuals. Thus *A. interioris* agrees with *A. pusilla* and *A. nullarborensis*, and differs from all the other species of *Austroicetes* of which sufficient material has been studied, in lacking the pattern morph *albomedia*. The absence of the morphs *acruiciata*, *posteroalba*, and *albolobalis*, so far known only from *A. pusilla*, should not be stressed, in view of their low frequency in the latter species.

The frequency spectrum is given in Table 2. The intrusion of subjective factors into the classification of many specimens as one or other morph makes it inadvisable to draw conclusions from relatively small differences between the frequency spectra of species analysed at different times, even where such differences are formally significant. Thus the spectrum for *interioris* is best compared with that for *pusilla* given in Table 3 of the present paper rather than with Table 19 of Key (1954). It may be seen from Table 2 that the three most numerous morphs are *rubiginosa*, *lineosa*, and *trilineata*, in that order, with *rubiginosa* much the most abundant and *nigrovirgata* relatively rare and equalled or exceeded by *transmaculata*. The spectrum for the female differs from that for the male principally in the lower frequency of *rubiginosa* and higher frequency of *lineosa*, and in the occurrence of 7·6 per cent. of green or partly green individuals, which must be regarded as environmentally induced modifications of one or other of the morphs (see Key 1954). Of the 11 females in this category, six suggest the pattern of *rubiginosa*, three that of *trilineata*, and two that of *lineosa*; i.e. there is no suggestion that the green individuals are derived predominantly from *nigrovirgata* and *trilineata*, as they appear to be in *Chortoicetes terminifera* (Key 1954).

Compared with *pusilla* ("all material" in Table 3), *interioris* shows considerably higher frequencies of *rubiginosa* and *lineosa* and lower frequencies of *trilineata* and *nigrovirgata*. However, if we consider only the Western Australian material of *pusilla* (Table 3), which, as we have seen, approaches much closer to *interioris* in its phenotypic characters than does material from the eastern States, we find that, although *interioris* still shows a much higher frequency of *rubiginosa* and a much lower

TABLE 3
FREQUENCY OF THE DIFFERENT PATTERN MORPHS AND OF GREEN INDIVIDUALS IN AUSTROICEDES PUSILLA

		All material												W.A. material										
		Males					Females					Males					Females							
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%			
All material																								
Males		109	35	0	7	87	0	175	27	0	9	4	4	2	0	0	0	0	459					
	%	23.7	7.6	0	1.5	19.0	0	38.1	5.9	0	2.0	0.9	0.9	0.4	0	0	0	0	0	0	0	0	0	
Females		97	54	0	0	64	0	161	35	0	12	4	6	2	1	2	21		459					
	%	21.1	11.8	0	0	13.9	0	35.1	7.6	0	2.6	0.9	1.3	0.4	0.2	0.4	4.6							
W.A. material																								
Males		14	1.2	0	0	4	0	25	3	0	0	0	0	0	0	0	0	0	0	0	0	0	58	
	%	24.1	20.7	0	0	6.9	0	43.1	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Females		15	20	0	0	1	0	13	3	0	1	0	0	0	0	1	0	6	60					
	%	25.0	33.3	0	0	1.7	0	21.7	5.0	0	1.7	0	0	0	0	1.7	0	10.0						

frequency of *trilineata*, yet the western *pusilla* agrees with *interioris* in having frequencies of *lineosa* and *nigrovirgata* respectively much higher and much lower than those in *pusilla* as a whole. The frequency of *lineosa* is actually higher in both sexes of western *pusilla* than in *interioris*. Thus the phenotypic approximation of western *pusilla* towards *interioris* is expressed also in their pattern morph spectra.

Measurements

Measurements and morphometric ratios for *A. interioris* are included in Key's Table 20. The specimens concerned are those designated "form 4" (except for the male from Yardea, S.A.) and "form 4-3". There is no suggestion of any significant difference between these measurements and the remainder, which refer to *A. pusilla*.

Geographical Variation

The only suggestion of geographical variation is the apparent restriction to New South Wales of phenotypes with an abnormally wide medial band on the internomedian area of the hind femur (see p. 67), and the differently shaped X-chromosome in the rather small number of males examined cytologically from South Australia, compared with its condition in New South Wales (p. 61).

Characters of Holotype and Allotype

In their morphological characters the holotype and allotype are typical of the species, except that the former is a little below average size. The cytology of the holotype is typical of an individual heterozygous for the Trangie rearrangement. Both specimens represent the pattern morph *ruginosa*, the allotype showing a tendency towards *transmaculata*. In their more diagnostic colour characters, the allotype is entirely typical, while the holotype has the medial band on the internomedian area of the hind femur a little wider than usual (but still well under twice the width of the proximal pale area) and continued proximally as a thin line. The hind tibia of the holotype is red in the distal half.

Distribution

See Section IV.

Specimens Here Recorded

In the following list, series not available to Key in 1954 are marked by an asterisk at the end of the relevant entry. The remainder were listed by him as "*pusilla*" (pp. 139-142). Males examined cytologically are recorded in bold-face type. All material is in the Division of Entomology Museum except 10 paratypes deposited in other museums as already indicated. Abbreviations of collectors' names are as listed by Key (1954, p. 237). MJDW=M. J. D. White.

QUEENSLAND: Tickalara H.S. (old), 4 miles NW. of (Summit of Grey Range), 18.v.1949, K, 1 ♀. Tickalara H.S., 6 miles W. of (Grey Range), 15.xi.1949, LJC, 1 ♀. Wompah Gate, 3 miles N. of, 7.xi.1946, K, 2 ♂, 1 ♀.

NEW SOUTH WALES: Barnato Lake, W. of Cobar, 4 miles NE. of, 9.v.1949, K, 1 ♂. Barnato Lake, W. of Cobar, 10 miles ENE. of, 9.v.1949, K, 1 ♂, 1 ♀. Barnato Tank, W. of Cobar, 1 mile NE. of, 24.xi.1949, LJC, 1 ♂, 2 ♀. Bielpajah, near Ivanhoe, 5 miles W. of, 31.x.1946, K, 1 ♀. Bielpajah, near Ivanhoe, 13 miles E. of, 31.x.1946, K, 2 ♂. Birkalla, near Canbelego, 8.v.1949, K, 3 ♂, 2 ♀. Birkalla, W. of Nyngan, 25.xi.1949, LJC, 2 ♂, 2 ♀. Bootra H.S., E. of Milparinka, 30.x.1949, LJC, 1 ♂. Bourke, c. 10 miles N. of, 11.x.1937, K, 1 ♂. Bourke, 13 miles SE. of,

26.x.1949, LJC, 2 ♀. Bourke, c. 13 miles S. of, 10.x.1937, K, 1 juv. Bourke, 19 miles N. of, Oct. 1940, K, 1 ♂, 3 ♀. Bourke, 20 miles SE. of, 26.x.1949, LJC, 2 ♂, 8 ♀. Broken Hill, Feb. 1941, CEC, 1 ♂, 2 ♀. Broken Hill, 6 miles NNE. of, 4.xi.1946, K, 1 ♂. Broken Hill to Wilcannia, March 1941, K, 1 ♂. Bundemar Sta., Trangie, 1940-41, LRC, 1 ♀. Calleen, 11 miles NW. of West Wyalong, 24.iii.1956, LJC, 2+2♂*. Canowindra, 2.5 miles SE. of, 24.xi.1945, LRC, 1 ♀. Cobar, 2 miles E. of, 24.xi.1949, LJC, 1 ♂, 1 ♀. Cobar, 55 miles N. of, 10.x.1937, K, 1 ♂. Cobabora, near Dunedoo, 11 miles SW. of, 9.xii.1948, KBK, 1 ♂, 2 ♀. Cobham Lake, 18 miles SSW. of, 18.xi.1949, LJC, 2 ♀. Condobolin, 3 miles NW. of, 24.iii.1956, LJC, 1+3 ♂, 3 ♀ (one the *allotype*)*. Condobolin, 13 miles SSE. of, 24.iii.1956, LJC, 1+3 ♂, 3 ♀*. Condobolin, 15 miles E. of, 7.iv.1956, MJDW, 1+3 ♂*. Coolabah, Nov. 1905, WBG, 1 ♀. Coolah, 1 mile N. of, 10.xii.1948, KBK, 1 ♂. Coolamon, 2 miles W. of, 27.xi.1945, K, 1 ♀. Cootamundra, 4.x.1937, K, 1 ♂. Cootamundra, 11 miles NE of, 26.xi.1945, K, 1 ♀. Cowra, 5 miles WSW. of, 1.xii.1948, KBK, 1 ♂, 1 ♀. Cowra, 15 miles NE. of, 1.xii.1948, KBK, 1 ♂. Darnick, near Ivanhoe, 25 miles NW. of, 1.xi.1946, K, 1 ♂. Dunedoo, 3 miles ENE. of, 9.xii.1948, KBK, 3 ♂, 4 ♀. Dunedoo, 6 miles WSW. of, 9.xii.1948, KBK, 2 ♂. Eurowie, N. of Broken Hill, 21.i.1945, LRC, 2 ♂. Eurowie, 2 miles N. of, 4.xi.1946, K, 1 ♂. Eurowie, 22 miles N. of, 4.xi.1946, K, 1 ♂, 1 ♀. Forbes, 25 miles SW. of, 12.xi.1954, MJDW, 5 ♂*. Forbes, 25 miles SW. of, 17.xi.1954, MJDW, 1 ♂*. Fowler's Gap, N. of Broken Hill, 19.xi.1949, LJC, 1 ♀. Fowler's Gap, N. of Broken Hill, 26-28.v.1954, MJDW, 2+2 ♂, 2 ♀*. Gamma, 2 miles W. of, 27.xi.1945, K, 1 ♀. Girilambone, 4 miles SE. of, 22.x.1949, LJC, 2 ♂. Girilambone, 6 miles NW. of, 22.x.1949, LJC, 1 ♂, 1 ♀. Gongolgon, 12.x.1937, K, 2 ♂. Goolma, 1 mile ESE. of, 8.xii.1948, KBK, 1 ♂, 1 ♀. Goolma, 9 miles W. of, 8.xii.1948, KBK, 1 ♂. Goolma, 13 miles E. of, 8.xii.1948, KBK, 1 ♀. Goombalbie (Warrego R.), 28.x.1949, LJC, 1 ♀. Grenfell, 3 miles ESE. of, 1.xii.1948, KBK, 3 ♀. Grenfell, 5 miles SSE. of, 1.xii.1948, KBK, 7 ♂, 2 ♀. Grenfell, 12 miles SSE. of, 1.xii.1948, KBK, 1 ♂. Grong Grong, 4 miles E. of, 27.xi.1945, K, 1 ♀. Hermidale, 2 miles E. of, 8.v.1949, K, 3 ♂, 3 ♀. Hillston, 9 miles SE. of, 29.v.1954, MJDW, 1 ♀*. Jacob's Well, W. of Cobar, 2 miles W. of, 23.xi.1949, LJC, 1 ♂, 3 ♀. Lake Gunyulka, E. of Wilcannia, 1 mile E. of, 23.xi.1949, LJC, 1 ♀. Lake Gunyulka, SE. of Wilcannia, 10.v.1949, K, 1 ♂, 5 ♀. Leadville, near Coolah, 3 miles ENE. of, 9.xii.1948, KBK, 1 ♀. Leeton, 22.ii.1936 (?), ALT, 1 ♂. Maude, 11.i.1955, MJDW, 1 ♂*. Menindie to Broken Hill, March 1941, K, 2 ♀. Miandetta, near Nyngan, 1 mile W. of, 8.v.1949, K, 1 ♀. Moama H.S., E. of Wilcannia, 2 miles N. of, 23.xi.1949, LJC, 2 ♂, 1 ♀. Moama Sta., SE. of Lake Poopalloe, 2 miles NNE. of, 10.v.1949, K, 2 ♂, 2 ♀. Mt. Dering, N. of Broken Hill, 3 miles ESE. of, 19.xi.1949, LJC, 1 ♀. Mt. Gipps, 9 miles ENE. of Broken Hill, 21.xi.1949, LJC, 1 ♀. Mt. Woolakulkra, E. of Wilcannia, 1 mile N. of, 23.xi.1949, LJC, 1 ♂. Mudgee, 5 miles NW. of, 8.xii.1948, KBK, 2 ?. Muswellbrook, 8 miles SW. of, 7.xii.1948, KBK, 1 ♂. Myall Mundi, 16.xi.1954, MJDW, 7 ♂ (genitalia examined in 6)*. Myall Mundi, 9.i.1956, LJC, 4 ♂ ("on compact red soil")*. Narwarre Sta., 33 miles SE. of Louth, 12-15.xii.1952, A. Halsey, 1 ♂, 2 ♀*. Netallie Hill, 10 miles W. of Wilcannia, 22.xi.1949, LJC, 1 ♀. Nevertire, 3 miles SE. of, 21.x.1949, LJC, 1 ♂. Nevertire, 5 miles SE. of, 7.v.1949, K, 1 ♂, 1 ♀. New South Wales, Nov. 1954, MJDW, 1 ♂*. Nyngan, 4 miles WSW. of, 8.v.1949, K, 2 ♂, 1 ?. Nyngan, 4 miles NW. of, 22.x.1949, LJC, 1 ♂, 2 ♀. Packsaddle Tank, 16 miles SW. of, 18.xi.1949, LJC, 1 ♂, 3 ♀. Parkes, 5.ii.1937, K, 2 ♀. Parkes (golf links), 30.iii.1946, ALT, 53 ♂, 24 ♀. Steam Plains Sta., Booroorban, 28.iv.1936, W. Mathews, 1 ♀. Tamworth, 5 miles S. of, 11.xii.1948, KBK, 2 ♂, 1 ♀. The Peak, W. of White Cliffs, 12.v.1949, K, 1 ♀. Tiboorburra, 23.v.1949, K, 3 ♂, 5 ♀. Tiboorburra, 2.xi.1949, LJC, 1 ♀. Tiboorburra, 1 mile N. of, 7.xi.1946, K, 1 ♂. Tiboorburra, 1 mile W. of, 16.v.1949, K, 1 ♂. Topar Hotel, E. of Broken Hill, 1 mile ENE. of, 22.xi.1949, LJC, 1 ♂. Topar Hotel, E. of Broken Hill, 5 miles WSW. of, 21.xi.1949, LJC, 1 ♂. Trangie, 16.xi.1954, MJDW, 2 ♂*. Trangie District, 1 ♀. Trangie Exp. Sta., NW. of Trangie, 15.x.1946, LJC, 1 ♀. Trewilga, 2 miles ESE. of, 19.xi.1954, K & LJC, 1 ♀*. Tullamore, 8.ii.1937, K, 1 ♀ ("Figured specimen (Key 1954, Fig. 23)"). Ungarie, 7 miles E. of, 24.iii.1956, LJC, 1 ♂ (*holotype*)*. Upper Horton, near Barraba, 7 miles NW. of, 21.xi.1946, K, 1 ?. Volo H.S., Lake Poopalloe, 2 miles SE. of, 23.xi.1949, LJC, 1 ♀. Volo H.S., Lake Poopalloe, 3 miles WNW. of, 23.xi.1949, LJC, 2 ♂, 2 ♀. Volo Sta., Lake Poopalloe, 5 miles WNW. of, 10.v.1949, K, 1 ♂. Wallabadah, 6 miles N. of, 11.xii.1948, KBK, 1 ?. Weethalle, 9 miles W. of, 23.v.1954, MJDW, 1 ♂*. Wellington, 6 miles NNE. of, 8.xii.1948, KBK, 1 ♂, 2 ?. Wellington, 7 miles NW. of, 8.xii.1948, KBK, 2 ?. West Wyalong, 4 miles ENE. of, 11.xi.1954, MJDW, 3 ♂*. White Cliffs, 11 miles S. of, 11.v.1949,

K, 1 ♂, 3 ♀. Wilcannia, 1 mile NW. of, 11.v.1949, K, 1 ♂. Wilcannia, 16 miles WSW. of, 22.xi.1949, LJC, 1 ♀. Wollar, near Mudgee, 10 miles E. of, 7.xii.1948, KBK, 2 ♀. Wongarbon, 12 miles SE. of Dubbo, 8.xii.1948, KBK, 1 ♂. Wood's Reef, near Barraba, 12 miles ESE. of, 14.xii.1948, KBK, 1 ♂. Worungil Tank, W. of Wilcannia, 3 miles E. of, 22.xi.1949, LJC, 1 ♂. Yanco, 2 miles N. of, 28.xi.1945, K, 2 ♂, 2 ♀. Yanco Glen, near Broken Hill, 8 miles NE. of, 4.xi.1946, K, 1 ♂. Yiddah, 1 ♂, 1 ♀.

VICTORIA: Ouyen, 1 mile SE. of, 4.xii.1945, K, 7 ♂. Renmark, 15 miles ESE. of, 10.i.1955, MJDW, 1 ♂*. Yatpool, 5 miles S. of, 4.xii.1945, K, 2 ♀.

SOUTH AUSTRALIA: Callington, 5 miles SSW. of, 24.xii.1954, MJDW, 1 ♀*. Cockburn, 9·6 miles W. of, 27.iii.1939, HGA, 1 ♂. Curnamona, 6.xii.1935, HGA, 1 ♀. Curnamona, 7.xii.1935, HGA, 1 ♂. Curnamona, 34 miles N. of, 24.iii.1937, HGA, 1 ♀. Kingoonyah, 12 miles E. of, 15.x.1947, JHC, 1 ♀. Koonamore, 7.xii.1935, HGA, 1 ♂, 1 ♀. Mt. Eba H.S., 2 miles SSW. of, 11.x.1955, LJC, 1 ♂*. Nackara, 8.i.1955, MJDW, 1 ♂*. Nackara, 4 miles SW. of, 8.i.1955, MJDW, 1 ♂, 2 ♀*. Outalpa, 12.xii.1935, HGA, 1 ♂, 1 ♀. Port Augusta, 11 miles SE. of, 7.i.1955, MJDW, 1 ♂*. Port Augusta, 13 miles SE. of, 7-8.i.1955, MJDW, 1+9 ♂, 9 ♀*. Tailem Bend, 10 miles SW. of, 5.xii.1947, JHC, 1 ♀.

References in the Literature

Specimens collected by L. R. Clark show that his ecological observations on "*Austroicetes pusilla*" (Clark 1949) cover both that species and *A. interioris*. It is unlikely that the present species is implicated in any other published work, apart from that of Key (1954).

AUSTROICETES PUSILLA (Walker)

Figs. 1(a), 2, 5(b), 6

Epacromia pusilla Walker, 1870, p. 778.

Chortoicetes pusillulus Rehn, 1907, pp. 447-8, fig. 4.

Chortoicetes vicina Sjöstedt, 1932, pp. 6-9.

Chortoicetes vicina f. *plana* Sjöstedt, 1935, p. 38.

Austroicetes pusilla, Key partim, 1954 (forms 1, 2, and 3 and north-eastern, south-eastern, and south-western races), pp. 126-42, figs. 24, 25.

Of the material referred to this species by Key, 150 males, 153 females, and one juvenile are now recognized as *A. interioris* (q.v.). This leaves 553 males, 519 females, and 15 juveniles. The great majority of these have been examined by us and their identification as *A. pusilla* confirmed at one or other of the levels of reliability already discussed. Doubt remains particularly in regard to the juveniles and to adults lacking both hind legs. A certain proportion of the original material had been distributed to other museums and was no longer available, but we believe that very little of this represents *A. interioris*. In addition to the material available to Key, we have examined 236 males, 136 females, and six juveniles.

The following corrections and additions may be made to Key's treatment of this species:

Morphology

Key's description can stand, except his references to the "inland race". A strong angulation at the first transverse sulcus of the pronotum as seen in profile is "unusual", as stated, but does occur in *pusilla* as now understood and is not confined to the "inland race".

Genitalia of male as in Figure 5(b), but variable in many points of detail. The differences between this figure and the corresponding one for *A. interioris* (Fig. 5(a)), while possibly representing definite trends, are not maintained consistently even within a sample of six individuals of each species; they are discussed under *A. interioris*. The differences from *A. nullarborensis* (Fig. 5(c)) seem to be a little more marked. The following are consistent within the sample of six individuals of each species: inner lobes of lophi of epiphallus larger than in *nullarborensis*, their distal margin straighter and longer and their mesoposterior angle sharper; rami of phallus with their dorsal portions longer relative to the aedeagal valves than in *nullarborensis* and less pointed, i.e. their anterior margin more convex in lateral view. In addition, the epiphallus as a whole is usually less splayed posteriorly, with the result that the slits beneath the inner lophal lobes are usually narrower and the apices of these lobes more closely approximated in dorsal or posterior view; the inner lobes are also usually directed more mesad and less dorsad than in *nullarborensis*. The dorsal aedeagal valves are usually slightly shorter and broader in lateral view, though they may be sharper apically.

Cytology (Figs. 1(a) and 2)

$2n\delta = 23$. Homozygous for a medium-sized metacentric chromosome presumably the result of a pericentric inversion. Smallest chromosome much shorter than the next larger. X-chromosome strictly acrocentric, its short arm minute and ordinarily not visible. Chiasma frequency per nucleus = c. 16·7. Many chiasmata interstitial; localization not evident. No structural polymorphism.

Coloration

Key's description of the more "stable" coloration can stand, except at two points: the ventrointernal area of the hind femur has only *very rarely* a reddish tinge on its inner margin in *pusilla* as now understood; and the distal half of the hind tibia is always straw (not "straw to red") in the male.

Amongst the new material examined is one female from Nanambinia H.S., near Balladonia, W.A., which represents the first record for *A. pusilla* of the pattern morph *leopardina*. Details of the pattern of this morph vary somewhat from species to species. The present specimen has the following peculiarities (cf. general description of the morph given by Key (1954, p. 32)): Dorsal surface of head pale greenish between the postocular lines, the usual black area restricted to a narrow transverse band between the eyes. Pronotal lobe with the upper pale band extending posteriorly to the third transverse sulcus; the upper dark band little narrower or less distinct on the metazona than on the prozona and not clearly confluent with the shoulder fascia; lower dark band represented by a trace. A horizontal black band extends from the eye to the frontal ridge, immediately below the ventral margin of the temporal foveole.

Table 3 shows the pattern morph frequency spectrum based on the material of *pusilla* now available, i.e. the material analysed by Key (1954, Table 19) *less* that referable to *A. interioris* and that subsequently distributed to other museums, *plus* the supplementary material. It may be seen that the portion of Table 3 headed

"all material" shows a higher frequency of *rubiginosa* and a lower frequency of *trilineata*, *nigrovirgata*, and *transmaculata* than Key's Table 19. The difference is probably due mainly to the subjective difficulty of classification, rather stricter standards having apparently been applied by us for recognition of the three last-mentioned more contrasted patterns as against the more unicolorous *rubiginosa*. The lower portion of Table 3 shows the frequency spectrum for the material from Western Australia only. This differs from the spectrum based on all the material in the much higher frequency of *lineosa* and the much lower frequency of *nigrovirgata*. Thus the geographical variation in the frequency spectrum noted by Key persists after exclusion of the material of *A. interioris*. It has already been remarked that this western frequency spectrum shows an approximation to that of *A. interioris* similar to the approximation in other phenotypic characters.

Measurements

The measurements given in Key's Table 20 refer to *A. pusilla*, as now understood, except for six of the seven specimens referred to "form 4" (not the male from Yardea) and the male referred to "form 4-3". These are *A. interioris*. The means and variances of Table 20 must be disregarded, although they are probably not uncharacteristic of *pusilla*, since there is no evidence of any significant difference between the two species in any of the dimensions or ratios studied.

Geographical Variation

Key's discussion under this heading appears to be generally sound in so far as it relates to *A. pusilla* as now understood, i.e. to forms 1, 2, and 3 and the north-eastern, south-eastern, and south-western races. However, the populations between the southern limit of the north-eastern race and the northern limit of the south-eastern race are left without a racial designation (see Key's Fig. 25); we propose to include these within the south-eastern race, which then adjoins the north-eastern along the line from Mungindi to Walcha. The references to "form 4" and the "inland race" should be deleted, as referring to *A. interioris*. The demonstration that all the supposed intermediates between form 3 and "form 4" are either one species or the other and almost all of them *pusilla* indicates a range of variation in the south-western race considerably greater than visualized by Key. This extends right from specimens showing an approximation to *A. nullarborensis* in their phenotypic characters (Key, p. 136), through typical form 3, to those indistinguishable from *A. interioris*. There seems to be a tendency for it to be expressed as a south-north (or coastal-inland) cline in the extent of black pigmentation. As such, it would correspond to the similar cline between the south-eastern and north-eastern races, although in the eastern cline the medial band on the internomedian area of the hind femur is more than twice the width of the proximal pale region in the male and usually reaches almost to the base of the area, while in the western cline this band is less than twice the width of the proximal pale region in the male, and usually about equal to it.

Distribution

See Section IV.

Specimens Here Recorded

Key's list (Key 1954, pp. 138–142) should be amended by the deletion of the series listed here under *A. interioris*. It will then still include a very few specimens of the latter species that had been distributed to other museums and are no longer available. The only ones clearly suspect in this regard are the five from Waukaringa, S.A.

The following list covers the supplementary material, all of which is in the Division of Entomology Museum. Conventions as in the *interioris* list.

NEW SOUTH WALES and AUSTRALIAN CAPITAL TERRITORY: Adelong, 3 miles NE. of, 21.ii.1951, K. & LJC, 1 ♂, 1 ♀. Adelong, 7 miles W. of, 20.ii.1951, K & LJC, 1 ♂. Balldale, 2 miles W. of, 12.xii.1950, JHC, 1 ♂. Boorowa, 4 miles SW. of, 16.i.1954, LJC, 1 ♂, 2 ♀. Boorowa, 10 miles N. of, 25.iii.1955, LJC, 2 ♂, 2 ♀. Boorowa, 13 miles N. of, 16.i.1954, LJC, 1 ♂. Calleen, 11 miles NW. of West Wyalong, 24.iii.1956, LJC, 2 ♂, 3 ♀. Canberra, 6.ii.1953, LJC, 1 ♀. Canberra, 2 miles S. of, 11.xii.1953, LJC, 2 ♀. Canberra, 5 miles E. of, 11.xii.1953, LJC, 1 ♀. Caragabal, 3 miles W. of, 1.iii.1956, LJC, 3 ♂, 1 ♂ juv., 1 ♀ juv. Condobolin, 13 miles SSE. of, 24.iii.1956, LJC, 2 ♂. Condobolin, 19 miles SSE. of, 24.iii.1956, LJC, 1 ♂. Forbes, 25 miles SW. of, 17.xi.1954, MJDW, 1+1 ♂ (genitalia examined in one). Gundagai, 4 miles S. of, 20.ii.1951, K & LJC, 1 ♂, 2 ♀. Gundaroo, 3 miles NNW. of, 18.ii.1954, LJC, 1 ♂, 1 ♀. Hall, 4 miles NNW. of, 5.i.1954, LJC, 1 ♀. Harden, 7 miles ENE. of, 16.i.1954, LJC, 1 ♀. Jeir, 1 mile NNW. of, 5.i.1954, LJC, 1 ♀. Marsden, 4 miles ESE. of, 1.iii.1956, LJC, 4 ♂, 2 ♀. Marsden, 9 miles NNE. of, 12.xi.1954, MJDW, 6 ♂. Miowera, 26.iv.1954, K & LJC, 1 ♂. Miowera, 3 miles ESE. of, 26.iv.1954, K & LJC, 1 ♂, 2 ♀. Moree, 4 miles E. of, 23.xi.1951, A. Dyce, 1 ♂, 2 ♀. Mt. Adrah, W. of Adelong, 2 miles SSE. of, 21.ii.1951, K & LJC, 1 ♂. Murrumburrah, 3 miles W. of, 26.xi.1945, K, 2 juv. Murrumburrah, 5 miles W. of, 29.ii.1956, LJC, 2 ♂. Myall Mundi, 10.vi.1949, LJC & B. Cameron, 1 ♂; 16.xi.1954, MJDW, 3 ♂ (genitalia examined); 9.i.1956, LJC, 6 ♂ ("on self-mulching soil"). Paddy's River, 16 miles NE. of Trangie, 26.xi.1953, LJC, 1 ♂, 1 ♀. Queanbeyan, 3 miles NW. of, 14.xii.1953, LJC, 1 ♂. Queanbeyan, 5 miles N. of, 14.xii.1953, LJC, 2 ♀. Stockinbingal, 4 miles E. of, 29.ii.1956, LJC, 1 ♀. Stockinbingal, 8 miles W. of, 29.ii.1956, LJC, 1 ♂. Sutton, 1 mile SSE. of, 18.i.1954, LJC, 1 ♂, 2 ♀. Sutton, 2 miles SW. of, 14.xii.1953, LJC, 1 ♂. Sutton, 6 miles S. of, 14.xii.1953, LJC, 2 ♀. Temora, 11 miles NNW. of, 1.iii.1956, LJC, 4 ♂. Trangie, 16.xi.1954, MJDW, 3 ♂ (genitalia examined). Trangie District, 1945, LJC, 1 ♀. Trangie Exp. Sta., NW. of Trangie, 15.x.1946, LJC, 1 ♂. Tumblong, 3 miles SE. of, 21.ii.1951, K & LJC, 1 ♀. Tumblong, 5 miles SW. of, 21.ii.1951, K & LJC, 1 ♂. Tumut, 2 miles NNE. of, 20.ii.1951, K & LJC, 1 ♀. Tumut, 13 miles NE. of, 20.ii.1951, K & LJC, 1 ♀. Wallendbeen, 1 mile E. of, 16.i.1954, LJC, 1 ♂. Wallendbeen, 6 miles W. of, 29.ii.1956, LJC, 2 ♂. Wee Jasper, 5 miles NE. of, 19.ii.1951, K & LJC, 1 ♂, 2 ♀. West Wyalong, 16 miles ENE. of, 12.xi.1954, MJDW, 1 ♂. Yagobie, E. of Moree, 5.xi.1951, A. Dyce, 1 ♀. Yass, 7 miles S. of, 19.ii.1951, K & LJC, 5 ♂, 2 ♀. Yass, 7 miles SE. of, 5.i.1954, LJC, 1 ♂, 1 ♀.

VICTORIA: Murchison, 5 miles W. of, 19.xii.1954, MJDW, 2 ♂, 1 ♀. Murchison, 6 miles W. of, 19.xii.1954, MJDW, 1 ♂.

SOUTH AUSTRALIA: Ardrossan, 5.i.1951, HMC, 1 ♂, 1 ♀. Black Springs, 1 mile S. of, 8–9.i.1955, MJDW, 1 ♂. Callington, 5 miles SSW. of, 24.xii.1954, MJDW, 2 ♂, 2 ♀. Cowell, 22 miles NE. of, 6.i.1955, MJDW, 1 ♀. Eudunda, 2 miles W. of, 9.i.1955, MJDW, 8 ♂, 2 ♀. Eudunda, 12 miles E. of, 9.i.1955, MJDW, 1 ♂, 3 ♀. Glen Osmond, 3 miles ESE. of, 15.i.1952, HMC, 18 ♂, 8 ♀, 2 juv. Goolwa, 6 miles N. of, 24.xii.1954, MJDW, 1 ♂. Lake Hamilton (S. end), 4.i.1955, MJDW, 3+1 ♂, 3 ♀. Laura, 5 miles N. of, 30.xii.1954, MJDW, 4 ♂, 1 ♀. Lowan Sta., 4 miles S. of Sherlock, 30.xi.1954, LJC, 1 ♀. Magill, 2 miles E. of, 18.i.1952, HMC, 1 ♂, 2 ♀. Morgan, 1 mile WSW. of, 9.i.1955, MJDW, 2 ♂, 4 ♀. Murray Bridge, 5 miles NNE. of, 28.xi.1954, LJC, 4 ♂, 3 ♀. Nackara, 8.i.1955, MJDW, 1 ♂, 1 ♀. Nackara, 10 miles SW. of, 8.i.1955, MJDW, 2 ♂, 1 ♀. Normanville, 2 miles SW. of, 25.xii.1954, MJDW, 2 ♂, 1 ♀. North Shields, 4 miles NW. of, 3.i.1955, MJDW, 7 ♂. Orroroo, 6 miles SE. of, 8.i.1955, MJDW, 1+1 ♂. Orroroo, 6 miles WNW. of, 8.i.1955, MJDW, 5 ♂. Port Augusta, 17 miles SW. of, 7.i.1955, MJDW, 1+1 ♂.

Port Wakefield, 4 miles NW. of, 28.xii.1954, MJDW, 3+5 ♂. Sherlock, 5 miles W. of, 25.xii.1954, LJC, 1 ♀. Tailem Bend, 3 miles SW. of, 24.xii.1954, MJDW, 9 ♂, 3 ♀. Tailem Bend, 3 miles NW. of, 24.xii.1954, MJDW, 5+2 ♂. Tumby Bay, 6 miles NE. of, 1.i.1955, MJDW, 2 ♂, 3 ♀. Two Wells, 2 miles NW. of, 28.xii.1954, MJDW, 5 ♂. Wangary, 4 miles SE. of, 4.i.1955, MJDW, 1 ♀. Whyalla, 28 miles SW. of, 31.xii.1954, MJDW, 6 ♂, 2 ♀. Wirrabara, 1 mile S. of, 30.xii.1954, MJDW, 1 ♂, 1 ♀.

SOUTH-WESTERN AUSTRALIA: Balladonia H.S., 11.xii.1953, JHC, 1 ♀. Bedonia Rk., 31 miles ENE. of Norseman, 8.xii.1953, JHC, 2 ♂, 5 ♀. Booanya Rk., 27 miles SSW. of Balladonia H.S., 12.xii.1953, JHC, 3 ♂, 4 ♀. Boorabbin, 1 mile W. of, 6.xii.1953, JHC, 1 ♂, 1 ♀. Broad Arrow, 4 miles N. of, 27.x.1954, JHC, 7 ♂, 5 ♀. Edah, 1 mile W. of, 21.x.1955, JHC, 7 ♂, 1 ♀. Fraser Range Gate, 57 miles E. of Norseman, 8.xii.1953, JHC, 1 ♂. Lake Magenta, 11 miles W. of, 5.ii.1953, JHC, 6 ♂, 1 ♀. Margooinya Rks., 4 miles WSW. of Balladonia H.S., 10.xii.1953, JHC, 4 ♂, 7 ♀. Menzies, 1 mile N. of, 28.x.1954, JHC, 5 ♂, 7 ♀. Nanambinia H.S., 5 miles S. of, 11.xii. 1953, JHC, 2 ♂, 4 ♀. Newman Rk., 22 miles ESE. of Fraser Range H.S., 9.xii.1953, JHC, 1 ♀. Norseman, 5 miles NW. of, 7.xii.1953, JHC, 1 ♂, 1 ♀. Norseman, 7 miles NE. of, 7.xii.1953, JHC, 1 ♂, 1 ♀. Nyabing, 6.ii.1953, JHC, 1 ♀. Paddington, 5 miles SE. of, 26.x.1954, JHC, 5 ♂, 1 ♀. Ten Mile Rks., 51 miles E. of Norseman, 8.xii.1953, JHC, 3 ♂, 3 ♀. Widgiemooltha, 12 miles NNW. of, 6.xii.1953, JHC, 2 ♂, 1 ♀.

NORTH-WESTERN AUSTRALIA: Minilya R., 3 miles NNE. of Minilya H.S., N. of Carnarvon, 14.vi.1953, JHC, 7 ♂, 3 ♀.

AUSTROICETES NULLARBORENSIS Key

Figs. 4, 5(c), 6

Austroicetes nullarboensis Key, 1954, pp. 142–62.

We have seen five specimens of this species additional to those available to Key. One male has been studied cytologically and the results reported earlier in this paper. Taken in conjunction with our findings on phenotypic intermediates between *A. pusilla* and *A. interioris*, they throw considerable doubt on Key's suggestion (1954, p. 143) that three specimens practically intermediate between *pusilla* and *nullarboensis* on the phenotype "may represent hybrids".

Male Genitalia

As in Figure 5(c), but variable in many points of detail. The differences from *A. interioris* (Fig. 5(a)) are inconstant and probably of no significance. Those from *A. pusilla* (Fig. 5(b)) are a little more substantial; they have been discussed under that species.

Cytology (Fig. 4)

$2n\delta = 21$. Homozygous for a large metacentric chromosome (which may be the same one as that present in *A. interioris*), resulting from a fusion. This chromosome shows 3–4 chiasmata at meiosis. Smallest chromosome much shorter than the next larger. X-chromosome metacentric, one limb about two-thirds the length of the other. Chiasma frequency per nucleus=c. 15–16. Localization of chiasmata not evident. The single individual examined did not show any structural heterozygosity.

Specimens Here Recorded

All material is in the Division of Entomology Museum. Conventions as in the *interioris* list.

SOUTH AUSTRALIA: Morgan, 1 mile WSW. of, 9.i.1955, MJDW, 1 ♂ (genitalia examined). Nackara, 8.i.1955, MJDW, 1 ♂ (genitalia examined).

SOUTH-WESTERN AUSTRALIA: Balladonia H.S., 11.xii.1953, JHC, 1 ♀. Balladonia H.S., 7 miles SSW. of, 11.xii.1953, JHC, 1 ♂ (genitalia examined). Youlgannah R.H., N. of Eyre, 8 miles E. of, 5.viii.1952, JHC, 1 ♂.

All the above localities are situated within the limits of distribution suggested by Key (1954, Fig. 20).

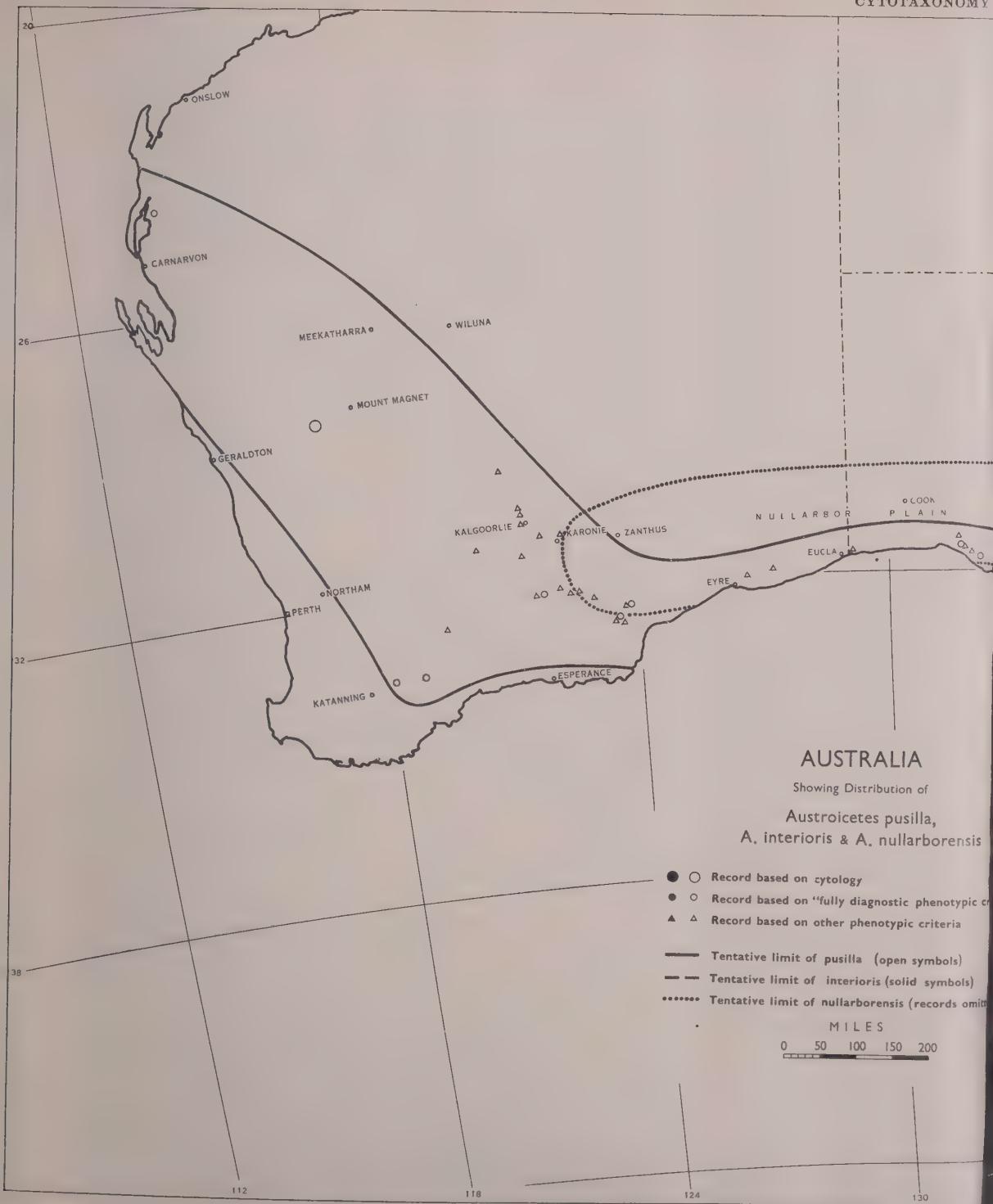
IV. DISTRIBUTION

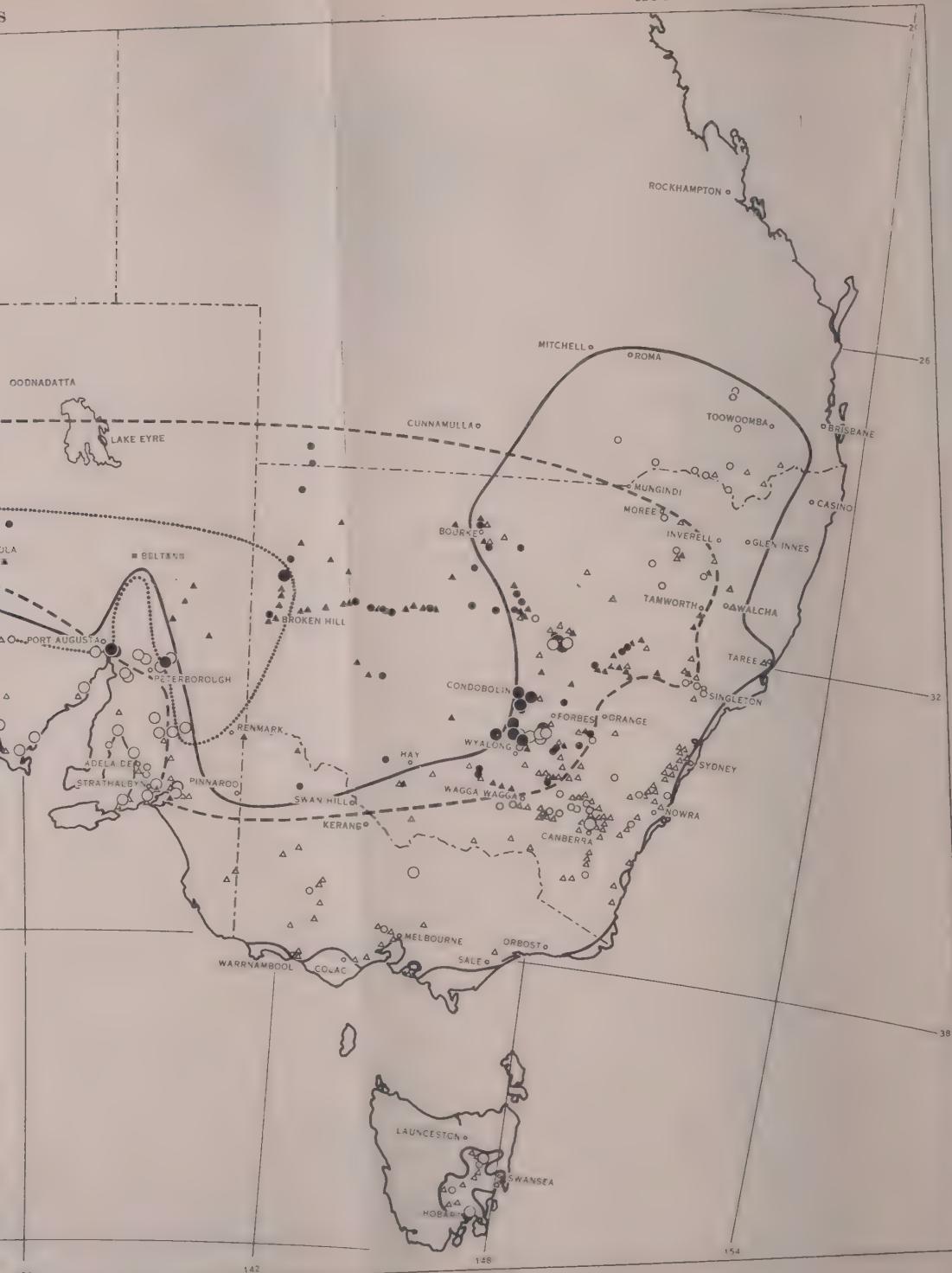
The distribution of *A. pusilla* and *A. interioris* is shown in Figure 6, different symbols being used to indicate the three reliability levels of the determinations. The distributional limits suggested lean only slightly on determinations made at the lowest reliability level, there being only two regions in which we may have erred substantially as a result of misidentifications. In the south-east of South Australia, the salient of *interioris* south-east of Adelaide rests on two females (from 5 miles SSW. of Callington and 10 miles SW. of Tailem Bend). The Callington female is entirely typical of *interioris*; it was collected with four other specimens, all identified as *pusilla*, two males being confirmed cytologically. The Tailem Bend female is not quite so typical, the medial band of the internomedian area of the hind femur being very slightly interrupted and the distal band on the ventrointernal area very dark but not complete.

There are two reasons for entertaining some doubts as to the correctness of these identifications: (1) the nearest other records of *interioris* are rather far removed from Callington and Tailem Bend, and are separated from those localities by several *pusilla* records; (2) three males from the vicinity of Tailem Bend, which were shown by cytological examination to be *pusilla*, had been misidentified on the phenotype as *interioris* and four others from the same area had been classed as intermediate (see Table 1). Nevertheless, in the absence of definite evidence to the contrary, we have regarded these two females as *interioris* and drawn the distribution limit of that species accordingly.

The second area where we may have erred is Western Australia. Only one series, from 1 mile W. of Edah, has been examined cytologically, and that proved to be *pusilla*, although one of the specimens had been identified as *interioris* on the phenotype. Thus no cytologically authenticated individual of *interioris* is known from Western Australia. The most westerly record based on fully diagnostic phenotypic criteria is that from near Mt. Eba H.S. in south-central South Australia, and it seems likely that the range of *interioris* does not extend far to the westward of this point. Three specimens from the shore of the Great Australian Bight and one from Karonie, W.A., which were recorded by Key (1954) as "form 4", may be *interioris*, but are not entirely typical, so that it is better to regard them as *pusilla*.

These uncertainties as to the geographic limits of *interioris* do not affect the general conclusions to be drawn concerning the relative distributions of the two species. It is clear that *pusilla* extends much nearer to the coast than *interioris* and has a clearly marked dry limit, whereas *interioris* occupies a more inland region and has no dry limit (Fig. 6). The additional records of *pusilla* alter its coastward limit, as mapped by Key, only in Eyre's Peninsula and south-western Western Australia.





The species is now known to occupy the whole of the Peninsula, the annual Meyer ratio* of which rises to about 100, and to extend south-westward in Western Australia to about the isopleth for that value. Its dry limit is at a Meyer ratio of about 30–70. Further collecting in eastern Queensland has failed to reveal *pusilla* north of Key's northernmost localities, so that the distribution has been given a tentative northern limit at the Great Dividing Range near Roma.

The distribution of *interioris* is of a rather different type from that of other species of *Austroicetes*. In South Australia it has a wet limit at a Meyer ratio of about 75, which is near the dry limit of *pusilla*. In New South Wales the wet limit becomes increasingly "wetter", until it reaches a Meyer ratio of about 160 near Mudgee and Inverell. Thus instead of the coastward limit of distribution running approximately parallel to the moisture isopleths or bending somewhat inland from them to the north, as it does in all the other species except *frater* (where it bends slightly coastward), it takes a more transverse or west-east course. Extensive collecting by one of us in the Alice Springs area, and especially by L. J. Chinnick both there and southward into South Australia, has failed to yield *interioris* further north than the northernmost records from south-western Queensland cited by Key. We have therefore suggested a northern limit for the species at about the latitude of Lake Eyre. Owing to lack of collecting in western South Australia and eastern Western Australia, we are unable to suggest where the western limit of *interioris* lies.

Although we have few new records of *nullarborensis*, the negative evidence from extensive collecting in Western Australia (J. H. Calaby) and South Australia (M. J. D. White and L. J. Chinnick) suggests that the distribution of this species does not extend far beyond the limit of the published records. It seems unlikely to occur west of about Karonie and is probably limited to the north by the latitude of the northern edge of the Nullabor Plain, as indicated in Figure 6.

Of the three species of the *pusilla* group, *nullarborensis* is the least tolerant of moist conditions, having a wet limit at a Meyer ratio of about 50 along its southern fringe, falling to barely 30 in the east, near Broken Hill. As we have seen, *interioris* has a limit (75) not much higher than this in south-eastern South Australia, the limits of the two species being separated by about 50 miles. But in the north-east *interioris* reaches a Meyer ratio of 160, and the two limits are over 500 miles apart. The two species overlap in a considerable area of east-central South Australia, which is nevertheless not a large fraction of the total distribution area of either. The dry limit of *pusilla* is such that this species overlaps narrowly with *nullarborensis* all along the southern fringe of the latter. The overlap with *interioris* is not much wider in the south-east of South Australia, but in north-central New South Wales it broadens to some 300 miles. The difference between the wet limit of *pusilla* in Western Australia (Meyer ratio about 100) and in the eastern States (260) is probably a racial one, as suggested by Key (1954).

These distributional differences indicate marked ecological and physiological differences between the three species. Although *nullarborensis* and *interioris* agree

* Defined as $P/s.d.$, where P is "normal" annual precipitation in in. and $s.d.$ the saturation deficit, in in. of mercury, calculated from the "normal" annual mean temperature and 9 a.m. relative humidity.

in requiring a more arid environment than *pusilla*, they diverge in opposite directions from the latter in another respect. Whereas *nullarborensis* appears to have no tolerance for moist conditions in the summer, *interioris* stands moisture much better in central-northern New South Wales, where there is a considerable component of summer rainfall, than it does in the strictly winter-rainfall areas.

The records now available show that a soil criterion cannot be used as a guide to the geographic distributional limits of *interioris* and, on the dry side, of *pusilla*, as was done by Key (1954, p. 137). On the other hand, the soil type does play a part in determining the ecological distribution of these species (see p. 59). The preference of *pusilla* for heavy soils appears only towards its dry limit, and in both species it is probable that the soil is an indicator of other habitat requirements rather than significant in itself.

A detailed revision of Key's (1954, p. 138) description of the distribution area of his "*A. pusilla*" must await more detailed comparative observations on the ecology of *pusilla* and *interioris*. The former is most abundant in grassland and savannah woodland on the tablelands of New South Wales and Victoria and was probably originally an insect chiefly of the savannah woodland. *A. interioris* reaches its greatest abundance (which is probably as a rule much below that of *pusilla*) further west, probably in cleared shrub woodland and tall woodland on the western slopes and plains of New South Wales. It was probably originally an insect of mallee savannah and shrub savannah.

V. DISCUSSION

The great difficulty experienced in separating *A. pusilla* and *A. interioris* on phenotypic criteria might suggest that they were species *in statu nascendi*, or at any rate forms which had diverged very recently. This kind of reasoning, particularly as applied to the species pair *Drosophila pseudoobscura* Frolova and *D. persimilis* Dobzhansky, has been rightly criticized by Mayr (1948). In that case the physiological and ecological differences between the two forms and their failure to hybridize in nature where their ranges overlap were regarded by Mayr as sufficient evidence against the view that they are "species in the making".

In the present instance the evidence is even stronger. All the kinds of differences mentioned above exist between *A. interioris* and *A. pusilla*. And, in addition, the very different genetic systems of these two grasshopper species suggest that they must have diverged in evolution a long while ago. Thus *interioris* has much less effective genetic recombination and its adaptive potentialities presumably depend more on a complexly coadapted chromosomal polymorphism, which, as we have seen, involves at least three autosomal pairs. On the other hand, *pusilla* must have far more crossing-over, but it lacks a system of chromosomal polymorphism, although the fact that it is homozygous for a pericentric rearrangement shows that it possessed such a system in the past, or is descended from a species that did. It is a more ecologically versatile species than *interioris*, with a continent-wide range, within which it has been able to adapt itself to a great variety of habitats. However, there is certainly no obligate relationship between amount of genetic recombination and ecological versatility—for example, *A. nullarborensis* has a high chiasma frequency, but is ecologically even more restricted than *interioris*.

If *pusilla* and *interioris* were vertebrates, it is probable that they would have been regarded as distinct species that hybridized in their zone of overlap. The demonstration of phenotypic overlap between *pusilla* and *interioris* in the absence of any hybridization—a demonstration particularly striking on account of the multiplicity of the cytological differences—necessarily inclines us to a rather sceptical attitude towards a number of claims to have established the existence of introgressive hybridization between animal species by classical taxonomic methods. Doubt seems particularly inevitable in those cases (such as the paradise flycatchers, studied by Chapin 1948) where the species show marked polymorphism and geographic variation, quite apart from the alleged hybridization in some geographic areas. The use of biometric criteria such as the "hybrid indices" employed by Sibley (1954) in his work on the towhees of Mexico is only an extension of classical taxonomic methods and can obviously be very misleading if one of the species is exhibiting genetic polymorphism for one or more of the characters that go to make up the index. A final verdict in such instances, where cytological evidence would be too difficult to obtain and might not be conclusive, will probably come from field studies of mated pairs.

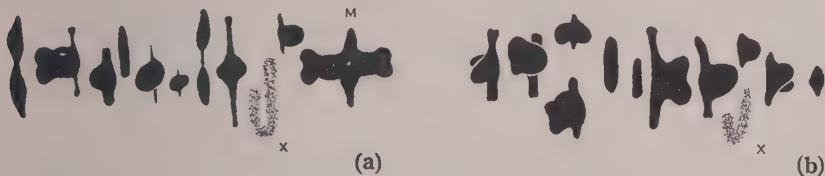


Fig. 7.—First metaphases in side view: (a) *A. tricolor* (1 mile N. of Banka Banka H. S., N.T.); (b) *A. tenuicornis* (16 miles ESE. of Katherine, N.T.). *M*, the large metacentric bivalent of *tricolor*, which has four chiasmata in this cell.

It is not possible from the cytological evidence to arrive at any firm conclusions as to the mutual relationships of the members of the *pusilla* group. The marked distal localization of the chiasmata in *interioris* is a feature not possessed by any other member of the genus. Both this species and *nullarborensis* have a large metacentric autosome, which is clearly the result of fusion. A similar chromosome is also present in *A. tricolor* (Sjöst.) (Fig. 7(a)). All these three consequently have $2n\delta = 21$ (instead of 23) and they all have a metacentric (J-shaped) X-chromosome. However, we cannot be certain that the same fusion is present in all three species—either in the sense of a fusion involving the same two elements, or in the sense of a fusion that has occurred once only in the evolution of the genus. In *nullarborensis* and *tricolor* the large metacentric autosome has a high chiasma frequency (3–4 chiasmata), while in *interioris* it always shows 2 chiasmata only. *A. tenuicornis* Key, which has been regarded as the species most closely related to *tricolor*, does not have an autosomal fusion (i.e. $2n = 23$), but its X is metacentric (Fig. 7(b)). The other species of *Austroicetes* (*vulgaris* (Sjöst.), *frater* (Branes.), *arida* Key, *cruciata* (Sauss.)) lack autosomal fusions and have acrocentric X-chromosomes. Autosomal pericentric rearrangements seem to occur only in the three members of the *pusilla* group. Thus the original stock of this group was certainly cytologically polymorphic. This polymorphism has been later lost in *pusilla* and perhaps also in *nullarborensis*, but is

retained and developed to a high degree in *interioris*. The J-shaped X-chromosome may quite likely have arisen independently in more than one phyletic stock—but if so the tendency in this group to develop mechanisms of adaptive polymorphism based on pericentric rearrangements is even more strongly marked.

From the phenotypic standpoint, we must regard *pusilla*, *interioris*, and *nullarborensis* as a compact species group, the members of which are more closely related to each other than to any other species of *Austroicetes*. The most closely related pair is *pusilla* and *interioris* and the most distant *interioris* and *nullarborensis*. The group shows a resemblance to *A. cruciata* through *nullarborensis* and to *A. tricolor* through *interioris*. Thus the phenotypic evidence would suggest a derivation of *interioris* from near the point of divergence of *pusilla* and *nullarborensis* in Key's phylogenetic tree (Key 1954, p. 232), and on the *tricolor* side of the *pusilla* branch. The simplest interpretation of the cytological evidence, on the other hand, would be that *pusilla* had diverged much earlier, before the establishment of the fusions present in *interioris*, *nullarborensis*, and *tricolor*, and perhaps even before the separation of *tenuicornis*. However, there is no reason to suppose that the simplest explanation is the true one, and *pusilla* could be derived from the *interioris-nullarborensis* stem by a dissociation of the large metacentric chromosome into two acrocentrics. Alternatively, independent fusions could have occurred in *tricolor* and the *nullarborensis-interioris* stock.

The cytological evidence also suggests, in this case without conflicting with the phenotypic evidence, that *cruciata* should be derived from the major trunk leading to the *vulgaris-arida* group and that *tenuicornis* and *tricolor* have split off independently from the trunk leading to the *pusilla* group, the former before and the latter after the establishment of the fusion. Under this arrangement the genus would be divided into two sections, one containing four species with all chromosomes acrocentric, and the other a group of five species with pericentric inversions and fusions prominent.

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A REVISION OF THE RUTELINE GENUS *ANOPLOGNATHUS* LEACH
(COLEOPTERA: SCARABAEIDAE)

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Summary

The genus *Anoplognathus* Leach is restricted to Australia and adjacent islands. Many of its species, commonly known as Christmas beetles, cause severe defoliation of trees, especially eucalypts. Notes on the biology, host preferences, and distribution of the species are given.

The key to the species is based on a careful study of their mutual affinities. The grouping that results differs considerably from that adopted by previous workers. The species are redescribed and figured, particular attention being paid to the male genitalia which show marked constancy within species, in contrast to the variation in colour, size, and degree of vestiture of the beetles.

The following new species are described:

- A. narmarus*, sp. nov.
- A. pindarus*, sp. nov.
- A. nebulosus moanus*, subsp. nov.

Changes of status proposed:

- A. insularis* Ohaus, 1898, to become a subspecies of *punctulatus* Oll., 1890.
- A. aurora* Arr., 1919, to become a subspecies of *macleayi* Blackb., 1891.
- A. acuminatus* Ohaus, 1904, to become a subspecies of *nebulosus* Macl., 1864.

New synonymies proposed:

- A. viriditarsis* Leach, 1815, = *reticulatus* Boisd., 1835, = *viridicollis* Macl., 1873.
- A. montanus* Macl., 1873, = *odewahni* Macl., 1873.
- A. olivieri* (Dalm.), 1817, = *duponti* Boisd., 1835.
- A. macleayi* Blackb., 1891, = *pallidus* Arr., 1919.
- A. rugosus* Kirby, 1818, = *longipennis* Macl., 1873, = *dispar* Macl., 1873.
- A. porosus* (Dalm.), 1817, = *pectoralis* Burm., 1844, = *luridus* Arr., 1901.
- A. hirsutus* Burm., 1844, = *explanatus* Arr., 1901.
- A. brunnipennis* Gyll., 1817, = *flavipennis* Boisd., 1835, = *quadrimaculatus* Ohaus, 1898.

I. INTRODUCTION

The author became interested in the genus *Anoplognathus* Leach when one of the four common species of the Canberra district (*A. montanus* Macl.) caused severe defoliation of eucalypts in the summer of 1949–50. Some observations were made then on the distribution, host plant preferences, and behaviour of this insect, while light-trap records of all four species were maintained in several subsequent years. Defoliation of eucalypts by other species was observed in various parts of New South Wales and Victoria, while from time to time specimens were received for identification from State forestry and agriculture departments. The defoliation problem was discussed by Jacobs (1950).

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Owing to their large size and often resplendent colouring, these insects were among the first to attract the attention of entomologists in the days of the exploration and settlement of Australia. Because of their great variability in colour and size, it was inevitable that many synonyms were created. Ohaus published a partial revision of the genus in 1904 and a catalogue in 1918. However, owing to the inadequate material of many species available to him, and to his lack of access to the Macleay types, his work contains several errors of identification. Moreover, additional species have since been described by Lea and Arrow, making a revision of the genus desirable. The need for this was reflected in the great number of wrongly identified specimens in most Australian collections, and it was also an essential basis for ecological studies.

Examination of material from all the major Australian collections and the loan of paratypic material from overseas museums, enabled the author to identify all the specimens he examined and to account for all the published names. He also selected types for the Macleay species from that author's type series; this was essential as some of these series are not conspecific.

The classification of the genus, proposed by Burmeister (1844) and followed by Macleay (1873) and Ohaus (1904), is unsatisfactory. Some of the group characters are difficult to employ and the classification that results places quite distant species in juxtaposition and separates others that are clearly very closely related. A new classification is here presented which groups the species in a way more truly reflecting their natural affinities and which finds independent support from characters of the male genitalia.

II. BIOLOGY AND ECOLOGY

Very little is known as yet concerning the biology or ecology of members of this genus. The adults feed on the leaves of trees, mostly eucalypts, while the larvae are soil-inhabiting forms that cause occasional damage to a variety of crops.

Observations were made on the common species of the Southern Tablelands of New South Wales, *A. montanus*, especially in the 1949–50 and 1955–56 seasons, when its numbers were extremely high. The larvae of this species commonly feed on rotting timber and are collected by turning over logs that have lain for several years. They also occur in the soil under natural pasture where they may feed on soil organic matter, grass roots, leaf mould, or the finer surface roots of eucalypts.

Eggs (approximately 25–30 per female) are laid from mid to late summer. The female compresses the soil about each egg so that it lies in a crude cell. The larvae hatching from the earlier-laid eggs are usually fully fed by the following spring and the next generation of adults emerges in early to midsummer; larvae from later-laid eggs may fail to pupate in the same year and these aestivate as fully grown larvae and do not pupate until the following season. Such prolongation of the larval stage occurs under unfavourable conditions, especially prolonged drought, and can be caused in the insectary by withholding moisture or by maintaining the larvae at temperatures below those obtaining in the field. The larvae pass through the three instars characteristic of all Scarabaeidae.

On hot summer mornings, the adults leave the ground and fly upwind towards trees; they fly vigorously and emit a characteristic buzzing note. Their outstretched elytra are very conspicuous, catching the light as the beetles hover about the upper foliage of trees. If the foliage is attractive, the beetles settle and begin feeding immediately. Copulation may occur at any time but is particularly frequent in late afternoon. The beetles have large, movable claws that enable them to grip the leaves securely even in high winds; they grasp the leaf blade or its petiole and move backwards as they feed, cutting in from the edge and often returning to the margin and thus excising a piece of leaf tissue. The ground beneath densely populated trees is often carpeted with such leaf fragments. The beetles will often completely destroy the immature leaves but when feeding on mature leaves they leave the midrib with irregular pieces of tissue attached. In late afternoon the number of beetles on the foliage decreases although there is no marked flight back to the soil; indeed, part of the population remains on the trees overnight and may be attracted to lights.

The damage done to individual trees was found to be influenced by factors such as their exposure, aspect, and the proximity of trees of other species of greater or lesser attractiveness to the beetles. There are obvious individual differences in attractiveness between trees of the same species or hybrid combination which are presumably of genetic origin. That the attractive factor is heritable is suggested by Pryor (1953). In Canberra *A. montanus* caused damage, particularly to *Eucalyptus rubida* Deane & Maid., *E. blakelyi* Maid., and *E. polyanthemos* Schau. Studies have been made of the damage to a large number of planted species and hybrids and it is hoped to present a report on this work in a separate paper.

In drier country to the west of Canberra, the species most concerned in defoliation of eucalypts is *A. pallidicollis* Blanch.; this species favours *E. albens* Miq., *E. melliodora* A. Cunn., *E. blakelyi*, and *E. camaldulensis* Dehn. In moister coastal districts, *A. viriditarsis* Leach causes severe defoliation of several eucalypts; *A. chloropyrus* (Drap.) is known to damage *E. dalrympleana* Maid., *E. dives* Schau., and *E. huberiiana* Naud. *A. olivieri* (Dalm.) has been recorded from the leaves of plum trees and *E. cladocalyx* F. v. M. *A. viridiaeneus* (Donov.) has been taken on the flowers of *Syncarpia laurifolia* Ten. near Sydney (Ohaus 1904).

Illingworth and Dodd (1921) observed defoliation by *A. boisduvali* Boisd. of several eucalypts, especially *tereticornis* (= *umbellata* Gaertn.) and *platiphylla* F. v. M. These authors also list host records for a number of other *Anoplognathus* species: *A. punctulatus* Oll. on the foliage of *Litsea ferruginea* (= *L. leefeana* (F. v. M.) Merr.) in the Cairns area, and on the young leaves of *Barringtonia calyptrata* R.Br. at Babinda; *A. aureus* Waterh. on *Hibiscus tiliaceus* L., *Tristemma virusanum* Juss., and *Breynia cernua* (Decne.) Muell.Arg. Mr. J. G. Brooks of Cairns has informed the author that he has taken *A. aureus* and *A. smaragdinus* Ohaus on *H. tiliaceus* at Cairns, *A. punctulatus* on the fruit of the avocado pear (*Persea americana* Mill.), and on the leaves of *Myristica cimicifera* R.Br., and *A. brunnipennis* Gyll. on *Eugenia* sp. The extensive literature on the insects associated with sugar-cane in Queensland (see Cumpston's 1941 bibliography) includes references to the following species: *boisduvali*, *punctulatus*, *aureus*, *pallidicollis*, *porosus* (Dalm.), *abnormis* Macl., and *parvulus* Waterh.

Christmas beetles are not regarded as major pests in any area and it is unlikely that it would be economically worthwhile to attempt their control except in special situations. The latter would include ornamental trees in streets and parks, or plantations set out as windbreaks or nurseries for reafforestation purposes. Repeated defoliation of mature trees undoubtedly reduces their life expectancy, although very few instances are known of trees whose deaths could be ascribed solely to beetle attack. Damage to young trees and saplings is quite significant in that defoliation prevents them from assuming their normal growth habit, and they tend to become rounded and bush-like, stunted, and with a mass of terminal shoots. An example of a defoliated tree is shown in Plate 1.

Effective protection of attractive species has been obtained by spraying them with 0·1 per cent. DDT emulsion at intervals of 2–3 weeks during the period December to February.

III. DISTRIBUTION

Ohaus (1904) comments (transl.): "Geographically the occurrence of the species of this genus seems to be limited to the eastern half of Australia and, as far as precise data of the localities are known to me, they do not extend to the west of Cape York in the north and Adelaide in the south."

While this statement is broadly true, there are at least two forms that are exceptions to it. *A. brevicollis* Blackb. is an inhabitant of the Northern Territory, while the subspecies *macleayi aurora* Arr. is known only from the north-west of Western Australia. *A. macleayi macleayi* Blackb. is known to the present author only from Central Australian localities although Ohaus describes a specimen reputedly from New South Wales. *A. rothschildti* Ohaus is a Queensland species but a single specimen of it in the British Museum is labelled with a locality in the extreme southwest of Western Australia, a distribution that seems highly improbable for a rare species; the author considers it to be almost certainly mislabelled. A single specimen of the common eastern species *porosus* is likewise labelled from the Northern Territory.

In Table 1 the known distribution records of all the species are tabulated; the dissection is based on the existing State boundaries with the exception that those parts of South Australia and the Northern Territory lying between latitudes 20 and 29° S. are designated as Central Australia.

Altogether 36 species and subspecies are recorded. Of these, 27 occur in Queensland, 11 being peculiar to that State. In New South Wales, 21 species occur, only 2 being peculiar. In Victoria, Tasmania, and South Australia there are 10, 4, and 2 species respectively: none are peculiar. New Guinea, the Northern Territory, Central, and Western Australia each possess a single peculiar form.

IV. TAXONOMY

Genus ANOPLOGNATHUS Leach

Anoplognathus Leach, 1815, Zool. Misc. 2: 43; Laporte, 1840, Hist. Nat. Col. 2: 125; Lacordaire, 1856, Gen. Col. 3: 369; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 353; Ohaus, 1904, Stettin. ent. Ztg 65: 67.

Paranonca Laporte, 1840, Hist. Nat. Col. 2: 143.

TABLE 1
DISTRIBUTION OF ANOPLOGNATHUS SPECIES
Doubtful records are indicated by queries

Species Group	Species	State or Territory								
		New Guinea	Qld.	N.S.W.	Vic.	Tas.	S.A.	Cent. Aust.	N.T.	W.A.
<i>montanus</i>	<i>viridiaceneus</i>	—	+	+	—	—	—	—	—	—
	<i>rhinastus</i>	—	+	+	—	—	—	—	—	—
	<i>viriditarsis</i>	—	+	+	+	+	—	—	—	—
	<i>montanus</i>	—	+	+	+	—	+	—	—	—
<i>macleayi</i>	<i>olivieri</i>	—	+	+	+	—	—	—	—	—
	<i>macleayi</i>	—	—	—	—	—	—	—	—	—
	<i>macleayi</i>	—	—	—	—	—	—	—	—	—
	<i>macleayi</i>	—	—	—	—	—	—	—	—	—
	<i>aurora</i>	—	—	—	—	—	—	—	—	+
<i>nebulosus</i>	<i>narmarus</i>	—	—	+	—	—	+	—	—	—
	<i>nebulosus</i>	—	—	—	—	—	—	—	—	—
	<i>acuminatus</i>	—	+	—	—	—	—	—	—	—
	<i>nebulosus</i>	—	—	—	—	—	—	—	—	—
	<i>moanus</i>	—	+	—	—	—	—	—	—	—
	<i>nebulosus</i>	—	—	—	—	—	—	—	—	—
	<i>nebulosus</i>	—	+	—	—	—	—	—	—	—
<i>porosus</i>	<i>rugosus</i>	—	?	+	+	+	—	—	—	—
	<i>porosus</i>	—	+	+	+	—	—	—	?	—
	<i>pindarus</i>	—	—	+	—	—	—	—	—	—
	<i>chloropyrus</i>	—	+	+	+	—	—	—	—	—
	<i>prasinus</i>	—	+	+	—	—	—	—	—	—
	<i>multiseriatus</i>	—	+	+	—	—	—	—	—	—
	<i>bisulcatus</i>	—	+	+	—	—	—	—	—	—
	<i>pallidicollis</i>	—	+	+	—	—	—	—	—	—
<i>concolor</i>	<i>concolor</i>	—	+	+	—	—	—	—	—	—
	<i>albomaculatus</i>	—	+	—	—	—	—	—	—	—
	<i>redescens</i>	—	+	—	—	—	—	—	?	—
<i>punctulatus</i>	<i>aureus</i>	—	+	—	—	—	—	—	—	—
	<i>punctulatus</i>	—	—	—	—	—	—	—	—	—
	<i>punctulatus</i>	—	+	—	—	—	—	—	—	—
	<i>punctulatus</i>	—	—	—	—	—	—	—	—	—
	<i>caeruleus</i>	—	—	—	—	—	—	—	—	—
	<i>semipunctatus</i>	—	+	—	—	—	—	—	—	—
	<i>caeruleus</i>	—	—	—	—	—	—	—	—	—
<i>calceatus</i>	<i>calceatus</i>	—	—	+	+	—	—	—	—	—

TABLE I (Continued)

Species Group	Species	State or Territory								
		New Guinea	Qld.	N.S.W.	Vic.	Tas.	S.A.	Cent. Aust.	N.T.	W.A.
<i>suturalis</i>	<i>suturalis</i>	—	+	+	+	+	—	—	—	—
	<i>hirsutus</i>	—	+	+	+	—	—	—	—	—
	<i>rubiginosus</i>	—	—	+	—	—	—	—	—	—
<i>brunnipennis</i>	<i>parvulus</i>	—	+	—	—	—	—	—	—	—
	<i>antiquus</i>	—	—	+	—	—	—	—	—	—
	<i>brunnipennis</i>	—	+	+	—	—	—	—	—	—
	<i>daemeli</i>	—	+	—	—	—	—	—	—	—
Species per State or territory		1	27	21	10	4	2	1	1	1
Peculiar species		1	11	2	—	—	—	1	1	1

Type species.—Leach (1815), in proposing the genus *Anoplognathus*, referred to it the species *viridiacneus* Donov. and a new species *viriditarsis* but did not designate a type species; *viridiacneus* Donov., 1805, is here selected.

The genus was succinctly characterized on the basis of the then-known species by Lacordaire (1856), while Ohaus published a revision in 1904, including a restatement of the generic characters. The following notes summarize the variation to be found in external morphology within the genus.

Head.—Clypeus of male usually narrowed towards anterior margin, the latter abruptly recurved and forming a deep apical truncated face; anterior margin usually distinct from the less strongly elevated lateral margins; sides convex, straight or concave in dorsal profile. Clypeus of female tending to a simple subquadrate or rounded form, sides and front being elevated to much the same degree. Size of antennal club subject to slight sexual dimorphism, that of the male being the larger. Head rarely strongly punctured in male but commonly so in female. Clypeofrontal suture approximately transverse, often slightly areuate anteriorly, or bisinuate. Ocular canthi slender, bearing white or pale brown setae.

Pronotum.—Anterior and basal angles usually well defined, the latter sometimes obtuse; sides evenly rounded or parallel in hinder portion and then contracted towards anterior angles; basal margin usually bisinuate; disc finely punctate in middle, more coarsely so and often rugulose at sides. Surface often with one or more pairs of slight impressions or flattenings of the weakly convex surface, usually with a median impunctate stripe or impressed line. Scutellum smooth or with sparse fine punctures.

Elytra.—Generally finely and lightly punctate, without well-developed discal or sutural striae; humeral calli poorly defined but subapical calli distinct and sometimes denticulate on hind margins. Epipleurae often dilated, flared, or thickened

TABLE 2

BODY LENGTHS AND MAXIMUM ELYTRAL WIDTHS OF BOTH SEXES OF EACH SPECIES OF
ANOPLOGNATHUS

Where less than 10 specimens of either sex were available, the actual number measured is quoted; in such cases, measurements given by Ohns (1994) were used as well as those of specimens examined by the author

Species	No. Exam- ined	Median Length (mm)						Maximum Elytral Width (mm)					
		♂			♀			♂			♀		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
<i>giganteus</i>	20	30	32	31.0	28	34	31.2	16	19	17.5	16	19.5	16.3
<i>g. cinctus</i>	25	19.5	25	22.6	22	27.5	24.2	12	14	13.1	13.5	16.5	14.2
<i>maculatus</i>	20	22.5	28	26.2	23.5	27.5	25.2	12.5	17.5	15.6	14	16	15.0
<i>montanus</i>	20	22	27	25.6	22	27	24.8	13	16	14.8	14	16	14.8
<i>obsoletus</i>	20	23	25	24.1	24	29	26.3	13.5	16	14.8	14.5	17.5	15.8
<i>m. maculatus</i>	45	27.5	29	28.1	26	28	27.5	14.5	15.5	15.0	15.5	16	15.6
<i>m. maculatus</i>	55	26	30	27.3	26	28.5	27.0	13.5	15	14.3	14.5	16	15.2
<i>m. maculatus</i>	35	26	30	27.3	26	28.5	27.0	13.5	15	14.3	14.5	16	15.2
<i>m. maculatus</i>	35	21	25	22.8	22.5	25	23.7	12	14.5	13.0	13	14.5	13.6
<i>m. maculatus</i>	20	20	22	20.9	21	24	22.9	11	12.5	12.0	11.5	14	13.2
<i>m. acuminatus</i>	25	20	24	22.0				11	13	12.6			
<i>m. moanus</i>	1♂ 1♀	20			24			11.5			12		
<i>brevicollis</i>	42				21.5	24	23.1				12.5	14	13.3
<i>rapax</i>	20	17.5	21	19.7	19.5	23.5	21.8	10.5	12	11.2	11.5	13	12.4
<i>porosus</i>	20	17	23	21.1	20	25	22.9	10	13	12.4	12	15	13.4
<i>politus</i>	20	20	24	21.8	21	26	23.5	12	13.5	12.7	12.5	16	14.3
<i>discrepans</i>	20	21	24.5	22.6	20	27.5	22.9	11	13	12.6	11	15	13.0
<i>politus</i>	20	19	23	21.0	21	26	22.7	11	12	11.7	13	14	13.4
<i>politus</i>	20	18	23	21.1	20	24	22.1	11	13	12.1	12	14	12.9
<i>concolor</i>	20	15.5	18	17.0	16	21	18.1	8.5	11	9.7	8.5	11	9.8
<i>abnormis</i>	20	12	14.5	13.5	13	17	15.0	6.5	7.5	6.9	7	9	7.9
<i>rotundicollis</i>	45	14.5	16	15.0	15.5	18	16.4	7	8	7.5	8	9.5	8.7
<i>arcuatus</i>	20	12.5	14	13.2	14.5	16.5	15.6	6.5	7.5	7.1	7.5	9	8.5
<i>p. punctulatus</i>	20	19	23.5	21.1	20.5	24	22.2	9.5	12	11.2	11	12.5	12.0
<i>p. insularis</i>	1♂	21	23		22			11.5	12		13		
<i>amaragrinus</i>	20	15	19	17.2	18	21	19.1	8.5	10	9.5	9.5	11	10.1
<i>genuinus</i>	25	30	30	30				16.5	17	16.7			
<i>callosus</i>	20	21.5	25	23.7	21.5	26.5	24.4	12.5	15.5	14.0	12.5	16	14.7
<i>callosus</i>	20	18	22	19.6	19	23	20.6	10.5	13	11.8	10.5	13	12.3
<i>callosus</i>	20	18	22.5	20.0	21	23.5	21.9	11.5	12.5	11.9	12.5	14.5	13.3
<i>cubopunctatus</i>	45	19	21.5	19.7	21			11	13.5	11.9	12.5		

TABLE 2 (Continued)

Species	No. Exam- ined	Median Length (mm)						Maximum Elytral Width (mm)					
		♂			♀			♂			♀		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
<i>parvulus</i>	20	16	18	16.7	16	19.5	17.6	8.5	9	8.9	8.5	10.5	9.9
<i>brunnipennis</i>	20	18	20.5	19.3	19	21	19.8	10.5	11.5	10.8	10	12	11.0
<i>antiquus</i>	{ 1♂ 1♀	22			24			13			13		
<i>daemeli</i>	{ 4♂♂ 3♀♀	17	20	18.2	17	22	19.0	9.5	11	10.0	10	12	10.6
<i>multiseriatus</i>	{ 2♀♀	21			19.5	21	20.2				11.5		
<i>prasinus</i>	{ 5♂♂ 3♀♀	18	20	19.0	21	22	21.5	10.5	11.5	10.8	12.5	14	13.2

above hind coxae, especially in females; usually serrate and bearing fine hairs anterior to apices; the latter contiguous, individually rounded, or produced.

Legs.—Fore tibiae bi- or tridentate, the teeth variable in acuteness and in angle to main axis of tibia, spurs very small; 1st segment of fore tarsus short in most males, elongate in all females. Middle and hind legs slender, tibiae rarely with distinct carinae, spurs short, and separated by 2-5 ciliae; apical truncated face of tibia frequently bearing an inner row of fine hairs investing base of tarsus.

Mesosternal process.—Of variable length and shape - short, broad, and rounded (*brunnipennis*); or short, acute, and densely clothed (*suturalis*); or long and extending to fore coxae. In latter case the process may be flat (*pallidicollis*) or markedly sinuate (*punctulatus*).

Thorax and abdomen.—Clothed with white hairs, especially at sides. Pygidium rarely strongly convex in lateral profile in male, more or less flat in female, frequently compressed at sides and in extreme lateral angles; surface glabrous or more commonly clothed with white hairs, always with some elongate coloured hairs borne on or near apical ridge.

The author recognizes a number of fairly well-defined species groups. These are listed in Table 1, where the linear order of the species is the same as adopted in the subsequent key.

Anoplognathus is readily distinguished from the most closely related genera *Calloodes* White and *Repsimus* Mael. by virtue of its toothed fore tibiae (edentate in *Calloodes*) and its normal male hind tibiae (grossly enlarged in *Repsimus*). Those species having poorly developed mesosternal processes are distinguishable from *Anoplostethus* Brulle and *Epichrysus* White by their possession of simple claws on the hind legs of both sexes, and by their much smaller size. From *Parischizognathus* Ohaus, *Anoplognathus* differs in having a distinct clypeofrontal suture. From the

remaining Australian genera of the tribe Anoplognathini, it differs in having a dorsally reflexed labrum.

The dimensions of each species are listed in Table 2. For each species the largest and smallest available males and females were taken, together with eight other randomly selected specimens of each sex. The body lengths were measured from the free margin of the clypeus to the apical ridge of the pygidium, or, if the latter were not visible from above, to the elytral apices. The elytra were measured at the point of maximum width; the actual position of measurement thus varied between species, sometimes between sexes of the same species.

In the descriptions that follow, the locations of the specimens examined are given only for new or rare species. Series of common species that are to be found in all collections, bearing the author's determination labels, may be seen in those collections marked with an asterisk in the list below.

Full label data are given only for new or very rare species. In the case of the Macleay types, these bear labels indicating only the locality and the identification. Selection of types from the type series in the Macleay Collection was based on (a) agreement between the label locality and the locality as published, and (b) agreement between the specimens themselves and the original description of the species.

The types of a number of earlier described species were not seen, and it is doubtful whether some of these are still in existence. In such instances, identifications were made by reference to the original descriptions and to the more extensive restatements published by Ohaus (1904). Fortunately, most of the species concerned are very distinct; their descriptions are here restated from the material examined by the author, carefully checked against the original descriptions for inconsistencies.

The various collections from which material was examined are referred to in the text by the following abbreviations:

* AM	Australian Museum, Sydney.
BM	British Museum (Nat. Hist.), London.
BSES	Bureau of Sugar Experiment Stations, Brisbane.
* CSIRO	Division of Entomology Museum, C.S.I.R.O., Canberra.
* MACL	Macleay Museum, University of Sydney, Sydney.
* NM	National Museum, Melbourne.
* NSWDA	New South Wales Department of Agriculture, Sydney.
QDAS	Queensland Department of Agriculture and Stock, Brisbane.
QM	Queensland Museum, Brisbane.
* QU	Queensland University, Brisbane.
SAM	South Australian Museum, Adelaide.
WADA	Western Australian Department of Agriculture, Perth.
WAM	Western Australian Museum, Perth.

KEY TO SPECIES OF THE GENUS ANOPLOGNATHUS

- I. Mesosternal process with apex level with, or surpassing, hind margin of fore coxae 2
- Mesosternal process shorter, clothed with long hairs, apex acute (e.g. Fig. 69) (*suturalis* species group) 27
- Mesosternal process very short, glabrous, flat, and broadly rounded at apex (e.g. Fig. 81) (*brunnipennis* species group) 29

2(1). Dorsal surface of body lacking adpressed white scales 3
 Dorsal surface of body with adpressed white scales. Clypeus of ♂ strongly contracted and upturned at apex (Fig. 73). N.S.W., Vic., S.A. 25. *velutinus* Boisd.

3(2). Fore tibiae very broad, almost impunctate, lateral teeth commonly almost at right angles to axis of tibia (e.g. Fig. 14) 4
 Fore tibiae less broad, bearing white hairs, lateral teeth at considerably less than right angles to axis of tibia (e.g. as in Figs. 25, 49) 9

4(3). Disc of clypeus setose (examine under critical illumination at magnification of 15–20 \times) (*montanus* species group) 5
 Disc of clypeus glabrous (*macleayi* species group) 8

5(4). Pygidium bright green; elytral apices individually rounded, giving rise to deep broad re-entrant angle 6
 Pygidium reddish brown with or without greenish golden reflections; elytral apices either contiguous or with, at most, a very small re-entrant angle, as in *montanus* (Fig. 7) 7

6(5). Clypeus with sides evenly concave in dorsal profile. Large metallic golden green species. 30–34 mm in length; pygidium coarsely rugulose over whole surface. N.S.W., S. Qld. coastal regions 1. *viridiaeetus* (Donov.)
 Clypeus as in Figure 2. Smaller (c. 20 mm in length) species, reddish brown with bright green reflections on head and pronotum; elytra with weak purple sheen. N.S.W., Qld. 2. *rhinastus* Blanch.

7(5). All abdominal sternites widely glabrous across middle; pronotum and elytra with strong greenish gold reflections; ♂ clypeus strongly contracted before apex (Fig. 3); genitalia as in Figures 5, 6. N.S.W., Qld. coast and adjacent tablelands .. 3. *virgatitarsis* Leach
 All abdominal sternites except last with continuous bands of conspicuous decumbent white hairs; ♂ clypeus only slightly contracted in middle; genitalia as in Figures 9, 10. S. Qld., N.S.W., Vic., S.A. 4. *montanus* MacL.

8(4). Elytral apices contiguous; pygidium smooth, greenish, with conspicuous pre-apical convexity and strong anal tuft of reddish brown hairs. Some elytral punctures underlain by dark pigmented spots. Coastal east. Aust. 5. *olivieri* (Dalm.)
 Elytral apices individually rounded, slightly produced; pygidium rugulose, dull reddish brown with green or purplish sheen, lacking a conspicuous tuft of anal hairs. Elytra without pigmented spots. Cent. Aust., W.A. 6. *macleayi* Blackb.
 Brownish yellow to brown forms, with pygidium purplish blue. Cent. Aust. 6a. subsp. *m. macleayi* Blackb.
 Brownish yellow with golden rose-pink sheen on head and pronotum, or coppery green all over; pygidium greenish. N.W. Aust. 6b. subsp. *m. aurora* Arr. (stat. nov.).

9(3). Coloration of dorsal surface non-metallic 10
 Coloration of dorsal surface a metallic gold, reddish brown, green, cherry red, blue, or violet (*punctulatus* species group) 24

10(9). Elytral apices non-contiguous and produced (Figs. 18–20) (*nebulosus* species group) 11
 Elytral apices contiguous but distally spinose (Fig. 24). N.T. 9. *brevicollis* Blackb.
 Elytral apices contiguous, not spinose (Fig. 37) (*porosus* species group) 14

11(10). Clypeus of *montanus* type (Fig. 3); ventral surface of mesosternal process flat (Fig. 8). S.A., western N.S.W. 7. *narmarus*, sp. nov.
 Clypeus of *porosus* type (Fig. 31); mesosternal process depressed, then recurved towards fore coxae (Fig. 32) 8. *nebulosus* MacL. 12

12(11). Elytral apices very strongly produced and markedly serrate (Fig. 19); pale brownish yellow form with greenish rose reflections on head and thorax. Qld. (Carpentaria) ... 8b. subsp. *n. acuminatus* Ohaus (stat. nov.)
 Elytral apices less strongly produced, dull yellowish brown or brown forms 13

13(12). Yellowish brown form, mesosternal process glabrous. N. Qld. 8a. subsp. *n. nebulosus* MacL.
 Dark brown form, mesosternal process setose at sides near apex. Banks I., Torres Str. 8c. subsp. *n. moanus*, subsp. nov.

14(10). Pygidium smooth in middle of disc (at least) 15
 Pygidium rugulose or punctate over whole disc 16

15(14). Pygidium very smooth, shining, with golden green reflections; elytra a uniform deep reddish brown, heavily punctate. N.S.W. coastal regions 10. *rugosus* Kirby
 Pygidium smooth but with white setae about margins and down mid line, with coppery red or greenish reflections. Qld., N.S.W., Vic. coastal and tableland regions. Highly variable in colour and size 11. *porosus* (Dalm.)

16(14). Pygidium without uniform clothing of white hairs 17
 Pygidium uniformly clothed with decumbent white hairs 19

17(16). Pygidium bearing mixed punctures and micropunctures, the former not confluent except near margins. N.S.W. southern tablelands 12. *pindarus*, sp. nov.
 Pygidium uniformly rugulose 18

18(17). Pygidium bright green; mesosternal process flat, slender, sharp; elytra without pigmented striae. S. Qld., N.S.W. coast and tablelands 13. *chloropyrus* (Drap.)
 Pygidium dull red-brown, with weak green or violet reflections; mesosternal process strongly built, curved; elytra with deeply pigmented striae. Qld., N.S.W. coast and tablelands 14. *boisduvali* Boisd.

19(16). ♂ clypeus of *porosus* type (Fig. 48) 20
 ♂ clypeus either evenly rounded or with anterior margin recurved to greater extent than sides (Figs. 56, 57) but never of *porosus* type 22

20(19). Green species 21
 Yellowish brown species. Qld., N.S.W., Vic. 17. *pallidicollis* Blanch.

21(20). Epipleurae yellow on posterior half, disc of elytra apple-green, hind tibial spurs separated by 2 ciliae. N.S.W., Qld. coastal regions 15. *prasinus* (Laporte)
 Epipleurae and elytral disc uniformly dark olive-green, or with a weak pink tinge; hind tibial spurs separated by 3 ciliae. Qld., N.S.W. coastal regions 16. *multiseriatus* Lea

22(19). Concolorous species with portions of elytra deficient in pigment, giving water-soaked appearance. Qld. and N.S.W. coastal regions 18. *concolor* Burm.
 Species with either dark patterned markings on head and pronotum, or with pronotal and scutellar margins conspicuously darkened 23

23(22). Head, pronotum, and elytra with patterned markings (Fig. 56). Qld. 19. *abnormis* MacL.
 Pronotal, scutellar, and elytral margins dark greenish brown, contrasting with general brownish yellow body colour; head as in Figure 57. N. Qld. 20. *rothschildti* Ohaus

24(9). Dorsal surface either pure gold, pure reddish brown, or a mosaic of these metallic colours. Cent. and N. Qld. coastal regions 21. *cureus* Waterh.
 Dorsal surface green, or rarely cherry red, blue, or violet 25

25(24). Clypeus setose, deflexed at sides (Fig. 61) 22. *punctulatus* Oll.
 Green species, with disc of elytra conspicuously punctate; hind tibial spurs separated by a single stout cilia. N. Qld. 22a. subsp. *p. punctulatus* Oll.
 Bronze-green species, with disc of elytra micropunctate only; hind tibial spurs separated by 2 fine slender ciliae. New Guinea 22b. subsp. *p. insularis* Ohaus (stat. nov.)
 Clypeus glabrous 26

26(25). Smaller species (15–21 mm in length), green, almost impunctate on dorsal surface. Rarely cherry red, blue, or violet. Pygidium glabrous. Qld. coastal regions 23. *smaragdinus* Ohaus
 Larger species (c. 30 mm in length), green, conspicuously punctate on dorsal surface; pygidium lightly setose. N. Qld. 24. *aeneus* Waterh.

27(1). Elytral apices contiguous; basolateral regions of pronotum always glabrous. N.S.W. Vic., Tas. 26. *suturalis* Boisd.
 Elytral apices individually rounded, giving rise to small re-entrant angle; basolateral regions of pronotum commonly setose 28

28(27). Clypeus and pronotum abundantly setose. ♂ genitalia as in Figures 70, 71. N.S.W., Vic. **27. hirsutus** Burm.

Clypeus almost, pronotum quite, glabrous. ♂ genitalia as in *suturalis* (Figs. 67, 68). New Eng. distr. of N.S.W. **28. rubiginosus** MacL.

29(1). Pygidium glabrous; dorsal surface of body pure greenish gold or reddish brown, or a mosaic of these two metallic colours. Qld. coastal regions **29. parvulus** Waterh.

Pygidium uniformly clothed with decumbent white hairs; dorsal surface of body with neither uniform nor metallic colouring **30**

30(29). Clypeus setose **31**

Clypeus glabrous, in ♂ with narrow reflexed apex (Fig. 80). ♂ genitalia as in Figures 78, 79. Qld. **32. daemeli** Ohaus

31(30). Whole body with white adpressed hairs (reminiscent of *velutinus*); yellowish brown species with dark markings on head (Fig. 83) and pronotum. N.S.W. coastal regions **30. antiquus** Arr.

Dorsal surface, other than head, glabrous; head and pronotum green, elytra yellowish or reddish brown. Qld., N.S.W. **31. brunnipennis** Gyll.

1. ANOPLOGNATHUS VIRIDIAENEUS (Donovan)

Fig. 1

Melolontha viridiaeneus Donovan, 1805, Gen. Ill. Ent., 1, pl. 1.

Anoplognathus viridiaeneus Leach, 1815, Zool. Misc. 2: 44, pl. 75, fig. 1; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 354; Ohaus, 1904, Stettin. ent. Ztg 65: 78.

Rutela caesareus Billberg, 1817, in Schöenherr, Syn. Ins. 1 (3), app. p. 58.

Rutela latreillei Gyllenhal, 1817, in Schöenherr, Syn. Ins. 1 (3), app. p. 59.

This is the largest and most resplendent of the Christmas beetles and is commonly known as the "King Beetle".

Golden green species with underlying reddish brown pigment; head, especially clypeus, with strong rose sheen; pronotum and scutellum pure greenish gold; elytra with pigment discernible beneath similar sheen; pygidium, coxae, and abdomen bright green; legs reddish brown, tarsi black.

♂. Length 30–32 mm. Clypeus with sides depressed, finely emarginate, converging to strongly recurved apex; apical truncated face very deep, almost glabrous; disc and anterior portion of frons with short, erect, pale setae, with confluent irregular punctation becoming sparser on frons. Ocular canthi bearing fine dark setae; clypeofrontal suture anteriorly arcuate.

Pronotum with anterior angles moderately produced, acute; sides parallel in basal half, contracted behind anterior angles; basal ridge continuous, bisinuate, the basal angles obtuse; disc micropunctate. Scutellum with submarginal garland of setiferous punctures, partially concealed by dense tuft of hairs protruding from beneath pronotum.

Elytra with white hairs at humeral angles, epipleurae glabrous, not or only weakly serrate near apices, the latter individually rounded, giving rise to a wide re-entrant angle, the ends of the sutures minutely denticulate; disc finely punctate, surface finely microreticulate except near scutellum, strongly impressed below and behind humeral calli.

Fore tibiae broad, 3-dentate, teeth at almost right angles to major axis, bearing sparse very small hairs. Hind legs glabrous, with few short ciliae on tibiae, the spurs separated by 3–4 fine ciliae.

Mesosternal process smooth, flat, glabrous in middle, apex acute but flat, overhanging hind margin of fore coxae. Abdomen with sparse fine hairs at sides, glabrous across middle. No postcoxal process present.

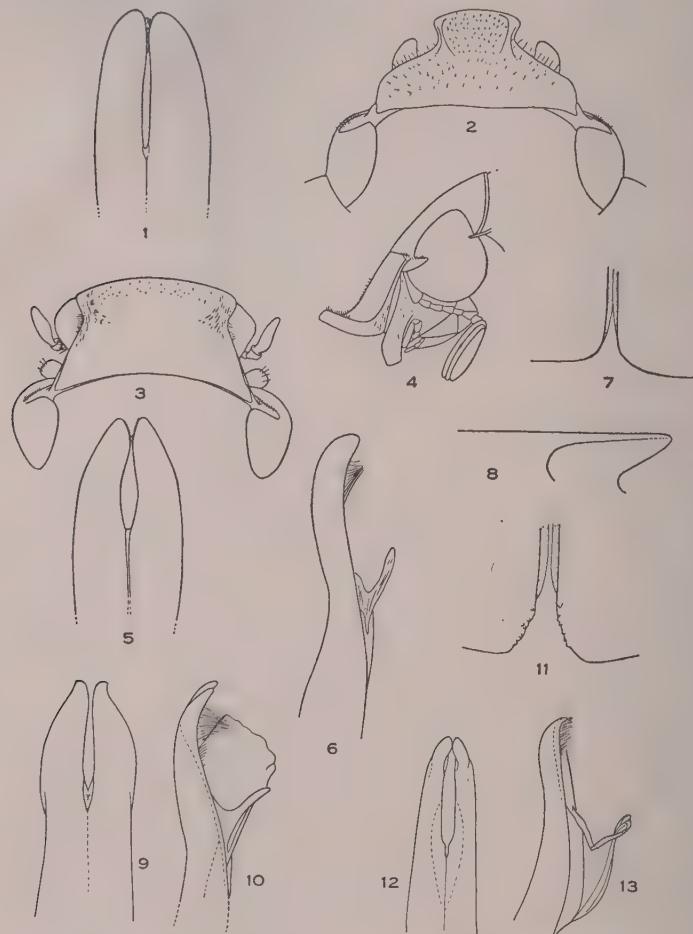


Fig. 1.—*A. viridiaeneus* (Donov.): gonostylar apices, dorsal. Fig. 2.—*A. rhinastus* Blanch.: ♂ head, dorsal. Figs. 3-6.—*A. viriditarsis* Leach: 3, ♂ head, dorsal (holotype of *viridicollis* Macl.); 4, ♂ head, lateral (holotype of *viridicollis* Macl.); 5, gonostylar apices, dorsal; 6, gonostyli, lateral. Figs. 7-10.—*A. montanus* Macl.: 7, ♂ elytral apices, dorsal (holotype); 8, ♂ mesosternal process, lateral; 9, gonostylar apices, dorsal; 10, gonostylar apices, lateral. Fig. 11.—*A. m. macleayi* Blackb.: ♂ elytral apices, dorsal. Figs. 12, 13.—*A. m. aurora* Arr.: 12, gonostylar apices, dorsal; 13, gonostylar apices, lateral.

Pygidium with numerous short pale hairs (visible only in oblique lighting), bright green, evenly rugulose, compressed at sides and in extreme lateral angles, apical ridge continuous, truncate, bearing rather short stout and sparse reddish hairs; disc gently convex in profile. Genitalia as in Figure 1.

♀. Length 28–34 mm. Clypeus with sides parallel, anterior margin rounded, evenly recurved. Head with coarser punctuation, pronotal ridges obsolete across middle. Elytra markedly compressed and more strongly punctate, epipleurae lightly setose at sides and strongly flared above hind coxae. Fore tibiae less broad, more strongly toothed; larger fore tarsal claws toothed. Pygidium flat, strongly compressed at sides.

Type locality.—Unknown. Boisduval refers to *caesareus* being found in the vicinity of Botany Bay, and *latreillei* as being found in many parts of Australia.

Type location.—Unknown.

Distribution.—QUEENSLAND: Brisbane, Ipswich, Sunnybank, Sunnybrook, Toowoomba, Woody Point. NEW SOUTH WALES: Dee Why, Lambton, Maroubra, Narrabeen, Peat's Ferry, Ramsgate, Undercliffe, Wahroonga. TASMANIA: "Tas." (mislabelled?).

Dates of collection.—November to February.

Specimens examined.—22 ♂♂, 13 ♀♀.

2. ANOPLOGNATHUS RHINASTUS Blanchard

Fig. 2

Anoplognathus rhinastus Blanchard, 1850, Cat. Coll. Ent. Col. p. 221; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 354; Ohaus, 1898, Stettin. ent. Ztg 59: 32; 1904, op. cit. 65: 79.

Ohaus (1918) placed *longipennis* MacL. as the probable female of this species. Examination of the type of *longipennis* has shown that this name refers to examples of *rugosus* Kirby.

Deep reddish brown species with green reflections: head, pronotum, and pygidium occasionally bright green.

♂. Length 19½–25 mm. Clypeus (Fig. 2) very narrow at base, strongly depressed, then elevated to a narrow, very abruptly recurved anterior margin, the latter extended hindwards by two ridges separated by a median concavity: apical truncated face very deep, this and anterior portion of clypeus very slightly setose: disc with fine punctures confluent except near clypeofrontal suture, the latter dark, transverse, sometimes with a weak posterior node in middle. Ocular canthi short, bearing yellowish brown setae. Frons shining, only appreciably punctate near suture.

Pronotum weakly convex, anterior angles rather acute, sides contracted behind them, basal margin bisinuate, the ridge almost continuous: disc with micro-punctures becoming larger and more conspicuous at sides, with a very fine, narrow, subobsolete median line. Scutellum large and micropunctate.

Elytra deep reddish brown with violet sheen at sides, quite heavily punctate, humeral angles with groups of hairs: epipleurae dilated above junction of meso- and metacoxae, finely serrate near apices, the latter widely rounded, giving rise to a deep re-entrant angle; subapical calli strongly developed, non-denticulate. Disc with punctures forming discernible striae and becoming coarser towards lateral margins.

Fore tibiae broad, strongly 3-dentate. Hind legs quite stout, femora glabrous, tibiae with stout dark ciliae, spurs separated by 2 fine ciliae: legs reddish brown with green sheen; tarsi black with blue sheen.

Mesosternal process glabrous, with greenish blue sheen, curved, tapering to acute apex overhanging mid fore coxae. Thorax with dense white villosity. No postcoxal prosternal process present.

Propygidium with fine white hairs across caudal margin: pygidium moderately convex in profile, with rather sparse transversely distorted punctures on disc, becoming rugulose at sides, with very sparse long pale brown hairs; sides and lateral angles slightly compressed, apical ridge continuous, apex and edge of last sternite bearing dense yellowish brown hairs. Abdomen black with green sheen and with sparse white hairs across middle.

♂. Length 22–27.5 mm. Clypeus slightly reflecting ♂ characters, coarsely and confluent punctate. Antennal club slightly shorter.

Pronotum broader, sides evenly rounded, not contracted behind anterior angles, basal angles rather rounded, disc with punctuation appreciably coarser.

Fore tarsi with larger claws toothed.

Epileurae with dilation as in ♂, disc with punctures smaller, less heavily impressed, subapical calli not as well defined, sides non-serrate near apices.

Type locality.—Unknown.

Type location.—Paris Museum (according to Ohaus).

Distribution.—QUEENSLAND: Brisbane, Bulimba. NEW SOUTH WALES: Prospect.

Specimens examined.—1♂, "Nevinson Coll. 1918-14, det. E. B. Britton" (BM); 1♂, 2♀, "Brisbane, Illidge", 1♂, "A. inustus? Bulimba" (QU); 1♀, "Prospect, N.S.W., 11-12-11" (NSWDA).

Macleay appears to have misidentified this species as he writes ". . . comes from Tasmania. I find two specimens of it in the collection of the late W. S. Macleay labelled as var. B of *analis*, a species which it much resembles."

3. ANOPOGNATHUS VIRIDITARSIS Leach

Figs. 3-6

Anopognathus viriditarsis Leach, 1815, Zool. Misc. 2: 44, pl. 75, fig. 2; Serville, 1825, Encycl. Meth. 10: 364; Macleay, 1827, Cat. Ins. Aust. King's Sd. Surv. 2: 440.

Rutela analis Dalman, 1817, in Schöenherr, Syn. Ins. 1 (3). app. p. 61.

Anopognathus analis Boisduval, 1835, Voy. Astrolabe, Col. 2: 169; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 354; Ohaus, 1898, Stettin. ent. Ztg 65: 83.

Anopognathus reticulatus Boisduval, 1835, Voy. Astrolabe, Col. 2: 169 (syn. nov.).

Anopognathus impressifrons Boisduval, 1835, op. cit. 2: 170.

Anopognathus viridicollis Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 357; Ohaus, 1904, Stettin. ent. Ztg 65: 82 (syn. nov.).

A specimen in the Macleay Museum from the type locality and agreeing with the description of *viridicollis* was selected as the type of that species by the present author. It is here placed in synonymy. *A. reticulatus* is similarly placed on the basis of its description and supplementary remarks by Boisduval who wrote (in transl.) "is very close to *A. analis*: possibly only a variety of smaller size in which the elytra appear to be less smooth, the scutellum a trifle more triangular and the underside of the abdomen in the male also more punctured and rugose than in *analis*."

The species is almost invariably known under the name *analis* in Australian collections. It is variable in size and colour and is widely distributed. It is closely related to *montanus* and its females are often difficult to distinguish from those of that species. Generally speaking, it appears to replace *montanus* in coastal areas and the higher rainfall districts of the eastern tablelands of New South Wales. The two species are sometimes found together in localities near the eastern limits of the tablelands.

Yellowish brown species with golden green reflections; abdomen, mesosternum, and tarsi black, the pygidium with a conspicuous tuft of long brownish yellow hairs.

♂. Length 22.5–28 mm. Clypeus (Fig. 3) with sides strongly concave in dorsal profile, the lateral ridges very strongly deflexed and not visible from above, anterior margin strongly recurved; apical truncated face glabrous, very deep (Fig. 4); disc with short inconspicuous erect golden hairs, the surface depressed and with fine shallow punctures; frons less densely punctate, vertex smooth; clypeofrontal suture anteriorly arcuate. Ocular canthi bearing white setae.

Pronotum rather flat, ridges almost continuous, the basal margin weakly bisinuate, the sides evenly rounded, anterior angles produced, basal angles obtuse; disc impunctate except at extreme margins, with a faint median impressed line. Scutellum impunctate, or with subobsolete submarginal garland of fine punctures.

Elytra with white hairs at humeral angles, epipleurae glabrous, not serrate, not flared, apices nearly contiguous, with a minute re-entrant angle; disc finely punctate, slightly compressed under humeral calli.

Fore tibiae broad, 3-dentate, the teeth at almost right angles to major axis, bearing very weak short hairs; hind legs with few stout ciliae on tibiae, the spurs separated by 2–5 fine ciliae.

Mesosternal process flat, or slightly elevated, brought to narrowly rounded apex overhanging hind margin of fore coxae. Abdominal sternites with white hairs at sides and with sparse pale brown hairs across middle.

Propygidium with small white marginal setae; pygidium abruptly convex in profile, usually bearing minute white hairs across base, the disc smooth and shining, with distorted punctures near margins, compressed at sides and in lateral angles, apical ridge concealed by dense tuft of yellowish or reddish brown hairs, these also present on hind margin of last abdominal sternite. Genitalia as in Figures 5 and 6.

♀. Length 23.5–27.5 mm. Clypeus evenly rounded, with rose reflections. Ocular canthi with white or pale brown setae. Elytra with epipleurae weakly flared above junction of meso- and metacoxae. Fore tibiae acutely 3-dentate, larger claws toothed; last abdominal sternite rugose. Pygidium much as in ♂ but the reddish hairs present only at apex.

Type localities.—Of *impressifrons* “near Botany Bay”; of *viridicollis*, “Darling Downs”. Others unknown.

Type locations.—♂ holotype, ♀ allotype of *viridicollis* in MACL. Others unknown.

Distribution.—QUEENSLAND: Brisbane, Darling Downs, Pialba, Roma, Stanthorpe, Toowoomba, Warwick. NEW SOUTH WALES: Armidale, Braidwood, Belmore, Bexley, Blue

Mountains, Castle Hill, Chatswood, Cook's R., Dee Why, Dorrigo, Ebor, Glen Innes, Gosford, Hayfield, Jindabyne, Kangaroo Valley, Kendall, Newport, Wollongong, Yowie Bay. VICTORIA: Bright, Brighton, Launching Place, Orbost. TASMANIA: "V.D. Land".

Dates of collection.—November to February.

Specimens examined.—Approx. 200.

4. ANOPLOGNATHUS MONTANUS Macleay

Figs. 7–10

Anoplognathus montanus Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 356; Ohaus, 1904, Stettin. ent. Ztg 65: 84.

Anoplognathus odewahni Macleay, 1873, op. cit. 2: 358 (syn. nov.).

After examination of the Macleay types of both *montanus* and *odewahni*, as well as a very long series of other specimens, the author is unable to admit of their being distinct, even at the subspecific level. The sole difference between the two forms is a greater degree of pygidial vestiture in the latter. There appears to be a gradient in this character, the most densely clothed specimens (such as the type of *odewahni*) occurring towards the western limit of the species. The name *odewahni* has page precedence over *montanus* but in proposing this synonymy, the author exercises his right as a "First Reviser" to select the more widely used and more euphonious name.

This is the most abundant of the *Anoplognathus* species occurring on the table-lands of south-east Australia. Enormous numbers feed on the leaves of eucalypts and are the cause of severe defoliation of both naturally occurring and planted trees. In Plate 1, the beetles are seen on a badly damaged specimen of *E. rubida* near Hall, A.C.T.

Light brownish yellow to reddish brown species with slight to intense purplish pink reflections; legs with a rose sheen; tarsi and abdominal sternites black; thorax and abdomen with white villosity beneath.

♂. Length 22–27 mm. Clypeus elongate with sides slightly concave, dilating behind abruptly recurved anterior margin; apical truncated face very deep, glabrous; disc with fine, short, erect, pale setae, surface finely and densely punctate, micro-reticulate. Clypeofrontal suture anteriorly convex; ocular canthi bearing white setae.

Pronotum with anterior angles obtuse, basal angles rounded, sides rounded, but subparallel in basal half, marginal ridges continuous even across bisinuate basal margin; disc finely and sparsely punctate, with a weak median stripe, weakly rugulose at sides and near anterior angles.

Elytra with humeral angles setose, epipleurae glabrous, non-serrate, weakly flared above hind coxae, apices individually rounded and producing a small re-entrant angle (Fig. 7); disc finely punctate.

Fore tibiae glabrous, 3-dentate, very broad, the teeth almost at right angles to major axis. Hind femora glabrous; tibiae without distinct carinae, spurs separated by 2 fine ciliae.

Mesosternal process (Fig. 8) black, flat, setose, with apex acute and overhanging hind margin of fore coxae. Postcoxal prosternal process lacking. Abdominal sternites other than last with continuous bands of decumbent white hairs across middle; last sternite slightly excised in middle.

Pygidium reddish brown, appreciably convex in profile, with shallow punctures becoming confluent at the sides; occasionally smooth in middle or with a median longitudinal impunctate stripe; apical ridge continuous, disc glabrous or with variable densities of short white decumbent hairs; strongly impressed at lateral angles; apical ridge bearing a tuft of brownish yellow hairs. Genitalia as in Figures 9, 10.

♀. Length 22–27 mm. Clypeus transverse, evenly emarginate, angles rounded; anterior truncated face setose, disc rugosely punctate, with many micropunctures.

Pronotum with sides evenly rounded. Elytra with epipleurae slightly flared above hind coxae, sparsely and finely setose. Pygidium less convex, tending to a sigmoidal profile. Larger fore tarsal claws toothed. Mesosternal process slightly deflexed at apex. Last abdominal sternite clothed.

Type locality.—“Monaro, Bathurst”.

Types.—♂ holotype, ♀ allotype selected from the Macleay type series bearing “Monaro” labels (MACL).

Distribution.—QUEENSLAND: Dalby, Gatton, Milmerran, Sunnybank, Stanthorpe, Toowoomba. NEW SOUTH WALES: Bathurst, Braidwood, Breakfast Ck., Canberra (A.C.T.), Cassilis, Cullerin, Howlong, Jindabyne, Mudgee, Mulwala, Orange, Queanbeyan, Rutherglen, Singleton, Tumut, Wahroonga, Wallendbeen, Wellington, Yass, Young. VICTORIA: Alexandria, Ararat, Bacchus Marsh, Cohuna, Dimboola, Heathcote Junction, Inglewood, Macedon, Mansfield, Monbulk, Ouyen, Warburton. SOUTH AUSTRALIA: Norwood.

Dates of collection.—November (S. Qld.) to March (Vic.). In Canberra, peak flights occur from early to mid January.

Specimens examined.—Approx. 1500.

5. *ANOPLOGNATHUS OLIVIERI* (Dalman)

Rutela olivieri Dalman, 1817, in Schöenherr, Syn. Ins. 1 (3), app. p. 60.

Anoplognathus olivieri Boisduval, 1835, Voy. Astrolabe, Col. 2: 172; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 354; Ohau, 1904, Stettin. ent. Ztg 65: 85.

Anoplognathus impressus Boisduval, 1835, op. cit. 2: 173.

Anoplognathus duponti Boisduval, 1835, op. cit. 2: 174 (syn. nov.).

The type of *duponti* could not be located. From its description it would appear almost certainly to be a small example of *olivieri*.

Brownish yellow species with golden green sheen on head, pronotum, scutellum, and to lesser extent on elytra. Pygidium dark brown with green reflections, abdomen green; remainder of lower surface reddish brown; tarsi a darker red-brown. Elytra with punctures underlain by pigmented zones, these tending to occasional longitudinal fusion. A very distinct and remarkably oval species.

♂. Length 23–25 mm. Clypeus with sides straight or weakly concave in dorsal profile, dilated at abruptly recurved anterior margin; anterior truncated face lightly setose, disc glabrous, with close or confluent punctures and micropunctures; frons similar in sculpture but with punctures less dense towards vertex; clypeofrontal suture dark green, curved anteriorly with a slight median flattening. Ocular canthi bearing white setae.

Pronotum with sides subparallel at base, moderately contracted towards slightly produced anterior angles, anterior margin with ridge stained green and continuous across middle; basal ridge obsolete across median bisinuation; disc

weakly convex, finely micropunctate, with a weak median impunctate stripe, surface with numerous micropunctures, microreticulate at sides.

Elytra with humeral angles weakly setose, epipleurae strongly serrate and weakly setose near apices, slightly flared over mesocoxae; apices nearly contiguous, slightly rounded, squarely cut; disc micropunctate, striae fairly evident, some punctures underlain by dark pigmented zones and these punctures more deeply impressed than the remainder.

Fore tibiae broad, bearing very short white setae, 3-dentate or with the basal tooth subobsolete; hind tibiae with both fine sparse white hairs and dark ciliae; spurs separated by 2 stout ciliae.

Mesosternal process setose at sides, depressed, sometimes recurved at apex, the latter narrowly rounded and overhanging fore coxae.

Propygidium with dense caudal fringe of white hairs; pygidium with hairs restricted to narrow basal area, the disc impunctate except for abundant long, fine, brown hairs at apex; apical ridge continuous, surpassed by highly convex carinate disc, the latter with green or purple reflections. Abdomen with white decumbent hairs at sides of sternites, widely glabrous across middle; last sternite slightly excised in middle.

♀. Length 28–30 mm. Clypeus more regularly emarginate, punctuation coarser, clypeofrontal suture straight. Pronotum with anterior ridge obsolete across middle, the disc micropunctate almost to margins. Elytra with epipleurae moderately flared over hind coxae. Larger fore tarsal claws toothed. Pygidial hairs sometimes present on mid line and behind apical ridge, leaving a pair of glabrous zones on disc (as in *porosus*); apex highly conical as in ♂, hind tibial spurs separated by 3 ciliae. Last abdominal sternite densely setose.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—QUEENSLAND: Bribie I., Brisbane, Bundaberg, Childers, Stradbroke I., Toowoomba. NEW SOUTH WALES: Avalon, Brunswick, Clovelly, Cronulla, Durrus Lake, Forster, Greenwich, La Perouse, Liverpool, Palmer's Channel, Queenscliff, Ramsgate, Roseville, Sydney. VICTORIA: Carrum, Half Moon Bay, Mansfield, Melbourne, Mordialloc, Seaford, Snowy R., Warrnambool. TASMANIA: “Tas.”

Dates of collection.—October (S. Qld.) to February (N.S.W., Vic.).

Specimens examined.—36 ♂♂, 31 ♀♀.

6a. *Anoplognathus macleayi* MACLEAYI Blackburn

Fig. 11

Anoplognathus macleayi Blackburn, 1892, Proc. Linn. Soc. N.S.W. (2) 6: 495; Lea, 1914, Trans. Roy. Soc. S. Aust. 38: 450.

Anoplognathus pallidus Arrow, 1919, Ann. Mag. Nat. Hist. (9) 4: 380 (syn. nov.).

This subspecies is known only from Central Australia. A paratype of *pallidus* is a typical example of it. As Arrow did not refer to *macleayi* in his comparative notes on *pallidus*, but only to *acuminatus* Ohaus, a much less closely related species, it seems probable that he overlooked Blackburn's species.

Large biscuit to dark brown species, elytra of lighter shade than head, pronotum, and scutellum; underside dark brown, without a coloured sheen; occasionally with slight violet sheen on legs.

♂. Length 28–29 mm. Clypeus of *montanus* type, elongate, with sides parallel in basal half, then dilated towards recurved anterior margin; truncated face deep, both this and disc glabrous. Head with dense fine subconfluent punctation; clypeofrontal suture anteriorly curved, with a slight median node; ocular canthi bearing white setae.

Pronotum with anterior ridge continuous, basal ridge obsolete across bisinuate median portion; disc with a shallow median impunctate stripe, elsewhere finely punctured except at sides where finely rugulose.

Elytra with epipleurae glabrous, serrations subobsolete, apices (Fig. 11) produced and forming a deep re-entrant angle, sometimes weakly serrate on their inner margins.

Fore tibiae broad, glabrous, with teeth nearly at right angles to axis of tibiae, often with traces of intermediate denticles. Hind legs glabrous, tibial spurs separated by 2 stout ciliae.

Mesosternal process flat, or slightly depressed, with finely rounded apex overhanging fore coxae.

Pygidium slightly convex in profile, disc glabrous, compressed at sides; apical ridge continuous, with sparse fine hairs. Abdomen with white hairs across mid line, the last sternite glabrous and with a deep median excision. Genitalia as in *m. aurora* Arr.

♀. Length 27½–28 mm. Head finely and quite confluent punctate; epipleurae flared above hind coxae; larger anterior claws toothed; hind tibial spurs separated by 3–4 ciliae. Abdominal sternites widely glabrous across mid line, the last with some hairs and excised as in ♂. Pygidium highly transverse, with abundant white, decumbent hairs directed towards mid line. Blackburn assumed his type to be a male on account of the wide membranous interval between the apical and penultimate abdominal segments but admits that the clypeus is of the female type. As the male clypeus is very distinctive, it is highly probable that the type is a female.

Type locality.—Basin of Lake Eyre, S.A. (*macleayi*); McDonnell Ranges, Hermannsburg, Cent. Aust. (*pallidus*).

Type locations.—Both in BM.

Specimens examined.—1 ♀, “Alice Springs, N.T., 16.3.1955, K.H.L.Key, at lights” (CSIRO); 1 ♂, “near Hermannsburg, C.A. 27.6.39, A. Musgrave”; 1 ♀, loc. cit. “28.6.39, Miss Cuthbert” (both AM). 1 ♀, “327, MacDonnell Ranges, C.A. 2.5.11, G. F. Hill” (NM); 3 ♀♀, “S. Australia” (MACL); 1 ♀, “Hermannsburg, Cent. Aust. H. J. Hillier, 1910–158, paratype? of *pallidus* Arrow, det. E. B. Britton” (BM); 1 ♂, 1 ♀, “Wells Exp., North-west S. Aust., Mar., 1903, H. Basedow, 6.12.03” (SAM).

Lea records the species from both the McDonnell Ranges and the Finke R. Ohaus described a specimen from Glen Innes, N.S.W., but the locality suggests that his specimen was mislabelled.

6b. ANOPLOGNATHUS MACLEAYI AURORA Arrow, stat. nov.

Figs. 12-15.

Anoplognathus aurora Arrow, 1919, Ann. Mag. Nat. Hist. (9) 4: 380.

This subspecies has the distinction of being the sole Western Australian representative of the genus. It is morphologically very close to typical *macleayi* but differs consistently in coloration and in distribution.

Light yellowish brown form with pale green and gold reflections on head and pronotum, rose reflections on elytra and legs; sterna, coxae, and abdomen reddish brown, with green reflections. Edges of clypeus darkened, clypeofrontal suture, ocular margins of frons, margins of pronotum, scutellum, and sutural margins of elytra stained green. Underside reddish brown to rose; tarsi brownish green to green, abdomen with green sheen towards caudal margins of sternites, pygidium with strong green reflections. Dorsal surface occasionally deep bronze with a strong green sheen.

♂. Length 26-30 mm. Clypeus large, slightly contracted at base, then sides parallel until suddenly dilated at abruptly recurved anterior margin; truncated face and disc glabrous, the latter closely and finely punctate, the punctures confluent and distorted at edge of clypeus and on ocular margins of frons; ocular canthi bearing white setae.

Pronotum with sides parallel in basal half, sometimes angulately contracted towards acutely produced anterior angles; ridge continuous across anterior margin, obsolete across bisinuate basal margin; disc with a weak median impunctate stripe, elsewhere discretely and finely punctate except at sides where overlaid by a fine rugulosity. Scutellum micropunctate.

Elytra glabrous, epipleurae serrate near apices, the latter produced and serrate on their inner faces as far as propygidium; disc evenly punctate, microreticulate.

Fore tibiae (Fig. 14) broad, distinctly 3-dentate. Hind legs slender, femora glabrous, tibiae without distinct carinae, spurs separated by 2 stout ciliae.

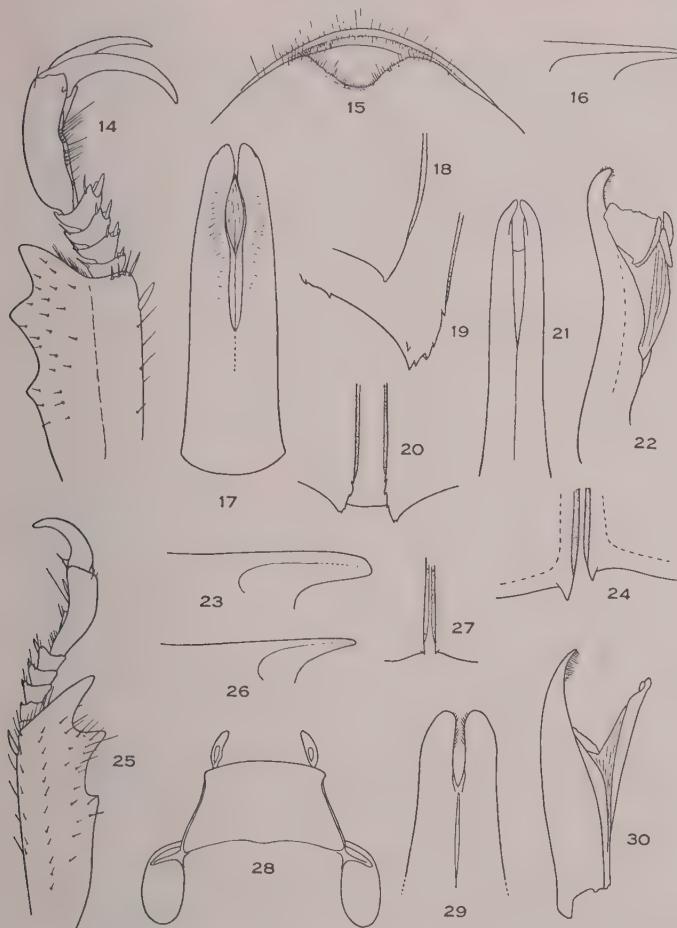
Mesosternal process slightly depressed and recurved, surface smooth and glabrous, apex overhanging fore coxae. Postcoxal prosternal process lacking. Abdominal sternites with short white hairs almost continuous across middle but sparse or lacking on last sternite; the latter deeply excised in middle (Fig. 15).

Pygidium rugulose, with decumbent white hairs most abundant near margins, apical ridge fine, continuous, bearing short but numerous reddish black setae; disc compressed at sides. Genitalia as in Figures 12, 13.

♀. Length 26-28.5 mm. Clypeus transverse, sides slightly convergent, angles rounded, anterior truncated face short, setose. Anterior pronotal ridge obsolete across median third. Epipleurae flared above hind coxae. Fore tarsi slender, the larger claws finely toothed at apices. Last abdominal sternite with lateral patches of white setae; pygidium uniformly clothed.

Type locality.—Tambrey, N.W. Aust.

Type location.—BM (holotype and 2 ♂ paratypes).



Figs. 14, 15.—*A. macleayi aurora* Arr.: 14, ♂ left fore tibia, dorsal; 15, ♂ last abdominal sternite, ventral. Figs. 16, 17.—*A. narmarus*, sp. nov.: 16, ♂ mesosternal process, lateral; 17, gonostyli, dorsal. Fig. 18.—*A. nebulosus moanus*, subsp. nov.: ♂ elytral apex, dorsal. Fig. 19.—*A. n. acuminatus* Ohaus, stat. nov.: ♂ elytral apex, dorsal. Fig. 20.—*A. n. nebulosus* Macl.: ♂ elytral apices, dorsal. Figs. 21, 22.—*A. n. moanus*, subsp. nov.: 21, gonostyli, dorsal; 22, gonostyli, lateral. Fig. 23.—*A. n. nebulosus* Macl.: ♂ mesosternal process, lateral. Fig. 24.—*A. brevicollis* Blackb.: ♀ elytral apices, dorsal. Figs. 25–30.—*A. rugosus* Kirby: 25, ♂ right fore tibiae and tarsus, dorsal; 26, ♂ mesosternal process, lateral; 27, ♂ elytral apices, dorsal; 28, ♂ head, dorsal; 29, gonostyilar apices, dorsal; 30, gonostyli, lateral.

Specimens examined.—♂ paratype; 1 ♂, “Jigalong, 28 miles E.N.E. of Mundiwindi, W. Aust. Dr. Gentilli” (AM); 1 ♂, 1 ♀, “100 miles N.E. of Roy Hill Stn., W.A., May 1946, McBolt”; 1 ♀, “Roy Hill Stn., W.A.”; 1 ♀, “Peak Hill, W.A.” (WADA); 1 ♂, 5 ♀♀, “Yandil”; 2 ♂♂, “Tambrey Stn.”; 1 ♂, “Mt. Edgerton”; 1 ♂, 1 ♀, “Wittenoom Gorge” (WAM).

The paratype examined has patches on the elytra, especially near the subapical calli, that appear darker, due to the local lack of yellowish brown pigment. The deep bronze specimens are from Roy Hill Station.

7. ANOPLOGNATHUS NARMARUS, sp. nov.

Figs. 16, 17

In colour this species is very similar to *brevicollis* Blackb. and to the paler examples of *m. macleayi* Blackb.

Pale biscuit with slight rose sheen on head; clypeofrontal suture and margins of clypeus dark brown; margins of pronotum golden. Legs yellowish brown with a coppery gold sheen; thorax and abdomen a deeper brown, the latter with a green sheen.

♂. Length 21–25 mm. Clypeus of *montanus* type, sides concave in dorsal profile, dilated at strongly recurved anterior margin; truncated face deep and sparsely setose. Margins deep brown, disc with short erect dense white hairs; clypeofrontal suture transverse, slightly curved anteriorly; frons glabrous; ocular canthi bearing white setae. Head with dense irregular shallow punctures, confluent except on vertex.

Pronotum weakly convex, sides parallel in basal half, anterior angles not produced, subacute, ridges widely obsolete across middle, basal margin bisinuate; disc with fine sparse punctuation, subrugulose at sides, with a weak median impunctate stripe and several paired lateral compressions. Scutellum glabrous, smooth, with golden edges.

Elytra with white hairs at basal angles, epipleurae bearing weak serrations and fine hairs near apices, the latter slightly produced, not contiguous, giving rise to a broad re-entrant angle; disc slightly compressed at sides, finely punctate, each puncture minutely pigmented, surface microreticulate.

Fore tibiae abundantly clothed with white hairs, acutely 3-dentate. Hind legs slender, femora and tibiae bearing white hairs, the latter with dark ciliae in addition; tibial spurs separated by 2 stout ciliae.

Mesosternal process (Fig. 16) usually flat, slender, rarely slightly sinuate, almost glabrous on mid line, apex with horizontal sharply rounded point overhanging mid fore coxae. Postcoxal prosternal process lacking. Coxae densely clothed. Abdomen with abundant decumbent white hairs across all segments, shortest and least numerous in middle.

Pygidium almost flat in profile, clothed uniformly with short white hairs directed towards mid line, surface uniformly rugulose, with coppery reflections; apical ridge continuous, stained green, bearing sparse long white hairs. Genitalia as in Figure 17.

♀. Length 22–25 mm. Clypeus subquadrate, finely and confluent punctate, most strongly elevated across anterior margin, with short, densely setose, apical, truncated face; fore tibiae more acutely 3-dentate, larger claws toothed. Epipleurae very slightly flared above hind coxae. Abdominal sternites glabrous on mid line.

Type locality.—Fowler's Gap, N.S.W.

Types.—Holotype ♂, "Fowler's Gap, 18 Nov. 1949, E. F. Riek" (CSIRO). Allotype ♀, "Hammond, S.A., I. H. Mincham" (AM). Paratypes: 1 ♂, 1 ♀, "Mananarie, S. Aust., ex. coll. S.A. Museum"; 1 ♂, "Broken Hill, March 1956, G. W.

Anson" (CSIRO); 1 ♂, "Broken Hill, C. E. Chadwick, 24.2.44"; 1 ♀, 8.3.1943, 1 ♂, 1 ♀, 16.4.1944, 2 ♀♀, 20.12.1944, all Broken Hill, G. W. Anson; 1 ♂, Broken Hill, 11.11.1944, 1 ♂, "Sth. Broken Hill, R. A. Cederblad, 27.11.46" (all NSWDA).

The trivial name is derived from an aboriginal word meaning "yellow".

8a. *ANOPLOGNATHUS NEBULOSUS NEBULOSUS* Macleay

Figs. 20, 23.

Anoplognathus nebulosus Macleay, 1864-5, Trans. Ent. Soc. N.S.W. 1 (Proc.): xix; 1873, op. cit. 2: 355; Ohaus, 1898, Stettin. ent. Ztg 59: 34; 1904, op. cit. 65: 104.

This is the most abundant of the subspecies of *nebulosus* here recognized. It is restricted in distribution to northern Queensland. Specimens from the Northern Territory identified as *nebulosus* have proved to be examples of *brevicollis* Blackb., a species incorrectly placed in synonymy with *nebulosus* by Ohaus (1918) in his catalogue.

Dorsally a uniform medium biscuit colour; underside darker, ranging from reddish brown to black with a coppery green sheen; surface, especially of elytra, with microreticulation. Legs reddish brown, tarsi black.

♂. Length 20-22 mm. Clypeus subparallel in basal third, then contracted toward recurved anterior margin; anterior truncated face short and glabrous, sides weakly emarginate, disc glabrous, finely rugulose; clypeofrontal suture dark, slightly curved anteriorly; frons glabrous, closely and finely punctate; ocular canthi bearing white setae.

Pronotum transverse, anterior angles subacute, not produced, both anterior and basal ridges obsolete across middle, the basal margin bisinuate and stained green; disc with close fine punctuation, finely rugulose at sides and with distinct impressed median stripe. Scutellum with edges green, its disc smooth.

Elytra sparsely setose at humeral angles, epipleurae glabrous, distinctly flared over mesocoxae; apices (Fig. 20) strongly produced, serrate both at sides on sutural margins; subapical calli denticulate; disc regularly and rather conspicuously punctate; sutural margins dark brown.

Fore tibiae broad, with pale yellow vestiture, 3-dentate, although with basal tooth small and sometimes almost obsolete, the other teeth poorly defined. Hind legs slender, tibiae without distinct carinae, spurs separated by 2 stout ciliae.

Mesosternal process (Fig. 23) smooth, glabrous, depressed, and moderately recurved, apex bluntly rounded and overhanging fore coxae; postcoxal prosternal process absent. Coxae and abdominal sternites with short white villosity, the latter sparse on abdomen, almost lacking on mid line.

Pygidium partly concealed by elytra, very slightly convex in profile; disc with even clothing of short, white, decumbent hairs and stout, erect, dark brown hairs near apical ridge, with vague greenish golden reflections.

♀. Length 21-24 mm. Clypeus with slight but continuous emargination, rather more pronounced in front than at sides. Epipleurae with serrations less well developed. Basal fore tibial teeth evident; anterior claws simple.

Type locality.—Port Denison, Qld.

Types.—♂ holotype and ♀ allotype selected from specimens from the type locality in MACL.

Distribution.—QUEENSLAND: Bowen, 12 miles S.E. of, Cairns, Cape York, Charters Towers, Chillagoe, Cooktown, Coomooboolaroo-Duarinya, Herberton, Hughenden, Marlborough, 63 miles N. of, Mutchilba, Mt. Isa, Northcote, Port Denison, Rockhampton, Somerset, Townsville.

Dates of collection.—May.

Specimens examined.—5 ♂♂, 16 ♀♀.

Collections.—AM; CSIRO; FEW; NM; SAM; QU.

8b. ANOPLOGNATHUS NEBULOSUS ACUMINATUS Ohaus, stat. nov.

Fig. 19

Anoplognathus acuminatus Ohaus, 1904, Stettin. ent. Ztg 65: 105.

This species, described by Ohaus as closely related to *nebulosus*, is here regarded as worthy of subspecific rank only.

Light brownish yellow species, with head, thorax, and scutellum darker and with rose-pink sheen.

♂. Length 20–24 mm. Clypeus with sides almost straight, converging from base then slightly dilated before abruptly recurved anterior margin; both deep apical truncated face and disc glabrous, the latter with fine shallow punctures; frons slightly more coarsely punctate and finely rugulose near margins, the surface bilaterally depressed behind clypeofrontal suture, the latter deeply pigmented at sides and curved slightly forward. Ocular canthi very slender, bearing short white setae.

Pronotum widest at basal angles, almost flat, anterior angles produced and acute, basal margin weakly bisinuate, the ridge obsolete across the middle; disc with fine sparse punctuation and narrow median stripe, with fine confluent punctuation near lateral margins; lateral ridges golden brown with pale green sheen. Scutellum smooth, impunctate, with brownish green margins.

Elytra pale biscuit, sutural margins dark brown with green sheen, epipleurae glabrous, very slightly flared over mesocoxae, conspicuously serrate near and on inner margins of apices (Fig. 19); disc finely and regularly punctate, slightly compressed below and behind humeral calli; subapical calli denticulate on posterior margins.

Fore tibiae slender, scarcely tridentate (the basal tooth subobsolete), with rose-gold sheen. Hind legs slender, almost glabrous, tibiae with stout black ciliae not forming distinct carinae, spurs separated by 2 such ciliae; tarsi dark brown with deep green sheen.

Mesosternal process stout, extending to mid fore coxae, strongly depressed at base, glabrous, deep brown. Abdomen dark brown with green sheen, with very sparse short white hairs across middle, surface depressed so that, with depression of mesosternum, the coxae appear to be elevated to an unusual degree. Pygidium surpassed by elytral apices, flat, brown with green sheen, and with fine regular short decumbent white hairs.

♀. Unknown.

Type locality.—Clonecurry, Qld.

Type location.—Unknown.

Specimens examined.—1 ♂, "Queensland, Burketown, March '98, Nevinson Coll. 1918-14, *A. acuminatus* Ohaus, det. Arrow from descr." (BM); 1 ♂, "Burketown, March 1898, A. P. Dodd" (QDAS).

8c. ANOPLOGNATHUS NEBULOSUS MOANUS, subsp. nov.

Figs. 18, 21, 22

This form differs from *n. nebulosus* Macl. in having rather more abundantly clothed thorax and hind femora, mesosternal process having sparse hairs at the sides near its apex, a general body colour of a much deeper brown with very distinct green-stained margins to the pronotum, scutellum, inner edges of the elytra, and the clypeofrontal suture. Tarsi black with a strong green sheen. Elytral apices as in Figure 18; ♂ genitalia as in Figures 21, 22.

♂. Length 20 mm. ♀. Length 24 mm.

Type locality.—Moa, Banks I.

Types.—♂ holotype, ♀ allotype "Moa, Banks Is., Torres Str. 11.1.20. W. McLennan, K.47162. At lights" (AM).

9. ANOPLOGNATHUS BREVICOLLIS Blackburn

Fig. 24

Anoplognathus brevicollis Blackburn, 1892, Proc. Linn. Soc. N.S.W. (2) 6: 493; Arrow, 1919, Ann. Mag. Nat. Hist. (9) 4: 380.

This species was incorrectly placed in synonymy under *nebulosus* Macl. by Ohaus in his 1904 checklist; he did not give his reasons for so doing in the text of his revision. Arrow (1919) pointed out that the two species are quite distinct.

♀. Length 21.5-24 mm. The author has seen examples only of this sex. Similar to females of *n. nebulosus* but of a somewhat paler biscuit colour, the pronotal and scutellar margins stained a brown or coppery red; the head, pronotum, and scutellum with faint rose reflections; sutural striae deep greenish black; elytra glabrous at humeral angles, epipleurae dilated above hind margin of mesocoxae and more strongly serrate near apices than in *n. nebulosus*, apices (Fig. 24) contiguous, squarely cut, and with the sutural intervals produced to form a pair of short but distinct spines. Clypeus slightly less elevated anteriorly than in females of *n. nebulosus*, clypeofrontal suture bilaterally pigmented; fore tibial teeth more acute, and pronotal margins slightly contracted in front of basal angles. Lateral pronotal asperate regions more restricted.

Type locality.—Burrundie, N.T.

Type location.—BM.

Distribution.—NORTHERN TERRITORY: Pine Creek, Katherine R., Cape Arnhem.

Specimens examined.—4 ♀♀.

Dates of collection.—March (Pine Ck.); August (Cape Arnhem).

Collections.—AM; CSIRO; NM.

10. *ANOPLOGNATHUS RUGOSUS* Kirby

Figs. 25-30

Anoplognathus rugosus Kirby, 1818, Trans. Linn. Soc. Lond. 12: 405; Boisduval, 1835, Voy. Astrolabe, Col. 2: 177; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 87.

Anoplognathus rugosus Boisduval *see* Macleay, 1835, Voy. Astrolabe, Col. 2: 177.

Anoplognathus longipennis Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 356 (syn. nov.).

Anoplognathus dispar Macleay, 1873, op. cit. 2: 357 (syn. nov.).

Ohaus mistakenly regarded *longipennis* as the female of *rhinastus* Blanch. The types of both *longipennis* and *dispar* MacL. were selected by the author from appropriate material in the Macleay Museum and both are undoubtedly synonymous of *rugosus*.

Yellowish brown to reddish brown species, elytra commonly a deeper red than pronotum; the latter, with head and scutellum, having golden green reflections. Legs yellowish brown with weak green sheen; abdomen other than last segment, thoracic sternites and tarsi black with green sheen; pygidium very smooth, shining, and golden green.

♂. Length 17.5-21 mm. Clypeus (Fig. 28) with sides evenly narrowed, straight, anterior margin reflexed and stained rose; apical truncated face setose. Head with sparse shallow punctures becoming subconfluent at sides; clypeofrontal suture straight or weakly carinate anteriorly. Ocular canthi bearing white setae.

Pronotum with anterior angles neither acute nor produced, basal ridge continuous or obsolete across middle, the margin bisinuate; disc smooth, sparsely punctate, without a median stripe.

Elytra with epipleurae glabrous, slightly flared above mesocoxae, non-serrate, apices (Fig. 27) contiguous, or very slightly rounded, almost squarely cut; disc with slight compression below humeral calli, with strongly impressed punctures producing the characteristic macroscopic appearance of the species.

Fore tibiae (Fig. 25) 3-dentate, the basal tooth small, surface smooth, with sparse honey-coloured hairs. Hind tibial spurs separated by 2 stout ciliae.

Mesosternal process (Fig. 26) flat, tapering, acute, extending to hind margin of fore coxae, more or less glabrous along mid line. No post coxal process present.

Abdomen with white hairs confined to sides; pygidium glabrous except for apical brown hairs, the ridge continuous, disc lightly and very sparsely punctate, micropunctate, smooth and glossy, strongly impressed in lateral angles. Genitalia as in Figures 29, 30.

♀. Length 19.5-23.5 mm. Head more coarsely and confluent punctate, almost rugulose. Fore tibiae 3-dentate, basal tooth larger; larger claws toothed. Elytra with epipleurae thickened above mesocoxae as in ♂.

Type localities.—*rugosus*: "Australasia"; *longipennis*: Petersham, N.S.W.; *dispar*: New South Wales; *viridicollis*: unknown.

Type localities.—Female holotypes of *longipennis* and *dispar* in MACL. Others unknown.

Distribution.—NEW SOUTH WALES: Blue Mountains, Botany Bay, Bulli, Cronulla, Gosford, Dee Why, La Perouse, Maitland, Mittagong, Narrabeen, Northbridge, Petersham, Sydney, Wetherangs. WATERFALL, VICTORIA: Chirnside, Wodonga. TASMANIA: "V.D. Land". Ohaus (1904) also gives Cocktown, Qld., and Mansfield, Vict., as localities of this species.

Dates of collection.—December (N.S.W.).

Specimens examined.—27 ♂♂, 24 ♀♀.

11. ANOPLOGNATHUS POROSUS (Dalman)

Figs. 31–34

Ruscia porosus Dalman, 1817, in Schöenherr, Syn. Ins. 1 (3), app. p. 63.

Anoplognathus porosus Boisduval, 1835, Voy. Astrolabe, Col. 2: 180; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 95.

Anoplognathus inustus Kirby, 1818, Trans. Linn. Soc. Lond. 12: 405.

Anoplognathus petrensis Burmeister, 1844, Handb. Ent. 4 (1): 443 (syn. nov.).

Anoplognathus juridus Arrow, 1901, Ann. Mag. Nat. Hist. (7) 7: 396 (syn. nov.).

This, the most variable of all *Anoplognathus* species, is rarely correctly identified in Australian collections, being confused especially with *pallidicollis* Blanch., *rugosus* Kirby, and *boisiwili* Boisd. Some specimens have the elytral punctures underlain by deeply pigmented spots, rendering them very similar in superficial appearance to *boisiwili*. *A. petrensis* Burm. has been placed in synonymy on the basis of its description and on specimens of *porosus* so identified by Macleay, Lea, Arrow, and others. The type of Arrow's species *juridus* is merely an unusually dark example of *porosus*. Ohaus (1904) refers to a black specimen in the Oberthür Collection.

Ranging from light or medium biscuit, with head and elytra possessing a strong greenish rose sheen, to a uniform dark brown. In the lighter specimens the elytral pigmentation is conspicuous as in *boisiwili*: pygidium rose or green; legs light brown with green sheen; tarsi black with green sheen; abdomen deep reddish brown with green reflections.

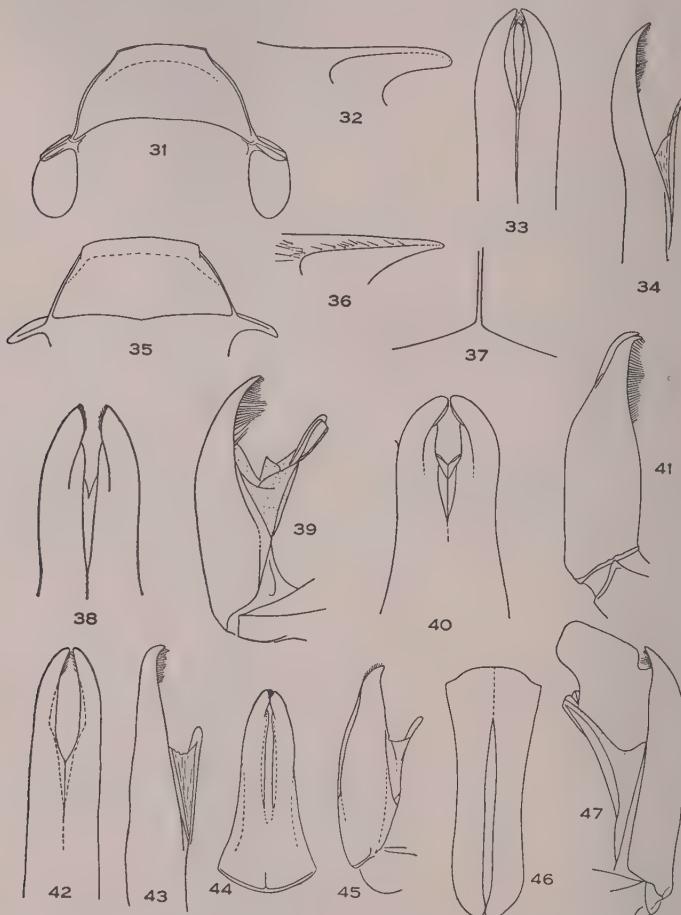
♂. Length 17–23 mm. Clypeus (Fig. 31) with sides convex in dorsal profile, narrowing towards shallowly recurved anterior margin; apical truncated face short and setose; disc with fine sparse punctation, clypeofrontal suture transverse, heavily pigmented at sides (contrast obscured in dark specimens).

Pronotum with sides parallel in basal half, not or only slightly contracted behind acute anterior angles; both anterior and basal ridges widely obsolete across middle, the latter with the margin bisinuate: disc very finely and sparsely punctate, denser towards lateral margins, lacking or with only a very faint median impunctate stripe, with bilateral impressed areas. Scutellum with margins stained a golden green, as also those of pronotum.

Elytra with humeral angles setose, epipleurae sparsely setose and moderately serrate near apices, the latter slightly produced, not quite contiguous and giving rise to a small re-entrant angle: sutural margins pale golden, disc with fine punctures underlain by dark pigmented spots; subapical calli denticulate on caudal margins.

Fore tibiae with sparse white hairs, 3-dentate. Hind legs slender, femora and tibiae with sparse hairs, the latter with ciliae forming vague carinae, the spurs separated by 2 fine ciliae.

Mesosternal process (Fig. 32) narrowly glabrous on mid line, depressed, apex recurved, narrowly rounded, overhanging mid fore coxae. Postcoxal prosternal process lacking. All abdominal sternites glabrous across middle.



Figs. 31-34.—*A. porosus* (Dalm.): 31, ♂ head, dorsal; 32, ♂ mesosternal process, lateral; 33, gonostylar apices, dorsal; 34, gonostyli, lateral. Figs. 35-39.—*A. pindarus*, sp. nov.: 35, ♂ head, dorsal; 36, ♂ mesosternal process, lateral; 37, ♂ elytral apices, dorsal; 38, gonostylar apices, dorsal; 39, gonostyli, lateral. Figs. 40, 41.—*A. chloropyrus* (Drap.): 40, gonostylar apices, dorsal; 41, gonostyli, lateral. Figs. 42, 43.—*A. boisduvali* Boisd.: 42, gonostyli, dorsal; 43, gonostyli, lateral. Figs. 44, 45.—*A. prasinus* (Lap.): 44, gonostyli, dorsal; 45, gonostyli, lateral. Figs. 46, 47.—*A. pallidicollis* Blanch.: 46, gonostyli, dorsal; 47, gonostyli, lateral.

Pygidium moderately convex in profile, smooth, shining, deep reddish brown with red or green reflections, compressed at sides and in extreme lateral angles, bearing erect brown hairs on and behind continuous apical ridge; disc bearing decumbent white hairs across base, along margins, and down a narrow median zone, leaving a pair of paramedian glabrous areas characteristic of the species. Genitalia as in Figures 33, 34.

♀. Length 20–25 mm. Clypeus truncate, head with coarser, confluent punctuation; pronotum with a weak impunctate median stripe. Clypeofrontal suture with slight median posterior node. Fore tibiae more acutely 3-dentate; larger fore tarsal claws toothed. Epipleurae conspicuously flared; abdomen with sparse erect pale brown hairs across otherwise glabrous mid line, these abundant on last sternite. Pygidium flat in profile.

Type localities.—*inustus*: “Australasia”; *luridus*: N.S.W.; others unknown.

Type locations.—*luridus*: BM; others unknown.

Distribution.—QUEENSLAND: Benarkin, Brisbane, Bulimba, Cairns, Chiltern, Cooktown, Cordalba, Farleigh, Gatton, Lawes, Mackay, Mapleton, Meringa, Nambour, Pialba, Rockhampton, Sandgate, Stanthorpe, Toowong, Toowoomba. NEW SOUTH WALES: Blackheath, Brigalong, Broken Head, Canberra (A.C.T.), Cassilis, Castle Hill, Cooma, Cullerin, Dorriga, Glen Innes, Glenfield, Gosford, Grafton, Guyra, Jenolan, Kangaroo Valley, Narara, National Park, Newcastle, Newport, Palmer's Channel, Pampoola, Port Stephen, Queanbeyan, Queenscliff, Richmond R., Singleton, Sydney, Thredbo R., Tubrabucca, Tweed R., Wahroonga, Wardell, Wollongong. VICTORIA: Ballarat, Bruthen, Mansfield, Melbourne, Orbost, Tallarook, Warburton, Wodonga.

Dates of collection.—October to February. The species has been collected in light traps at Black Mountain., A.C.T., where peak flights occur in mid January.

Specimens examined.—Approx. 500.

12. ANOPLOGNATHUS PINDARUS, sp. nov.

Figs. 35–39

This species is extremely abundant in the Canberra, A.C.T., and Queanbeyan, N.S.W., districts but has not been recorded from any other localities, except for a single isolated record from Bathurst, N.S.W.

Light reddish or yellowish brown species with a faint greenish sheen. Mouthparts and abdomen black; coxae and thoracic sternites reddish brown, the legs similar but with a green sheen, the tarsi darker; pygidium dark reddish brown with a characteristic dull green iridescence; abdomen with abundant white hairs at sides, sparse on mid line.

♂. Length 20–24 mm. Clypeus (Fig. 35) only slightly narrowed, the sides slightly convex in dorsal profile before the recurved anterior margin; apical truncated face short and setose. Head glabrous, finely and very closely punctate, with abundant micropunctures; clypeofrontal suture transverse. Ocular canthi bearing white setae.

Pronotal ridges widely obsolete across middle, sides rounded or slightly angulate before anterior angles, the latter neither acute nor produced; disc with sparse fine punctures becoming coarser and denser at sides, and interspersed with micropunctures, with a faint median impunctate stripe. Scutellum smooth.

Elytra with humeral angles glabrous; epipleurae non-serrate, with very fine setae near apices; the latter contiguous but not squarely cut (Fig. 37); disc finely punctate.

Fore tibiae 3-dentate, surface coarsely punctate and bearing white hairs. Hind legs slender, lightly setose, tibial spurs separated by 2 stout ciliae.

Mesosternal process (Fig. 36) flat, or slightly depressed, tapering, setose across middle behind apex which overhangs fore coxae. Postcoxal prosternal process lacking.

Pygidium slightly to moderately convex in profile, bearing sparse short white hairs, with punctures and very numerous micropunctures producing its characteristic dull appearance, with longer pale erect hairs near continuous apical ridge, slightly compressed at sides and in lateral angles. Genitalia as in Figures 38, 39.

♂. Length 21–26 mm. Head confluent, almost rugulously punctate, rather concentrically so about clypeofrontal suture. Larger fore tibial claws weakly toothed. Anterior clypeal margin more elevated than sides.

Type locality.—Black Mountain, A.C.T.

Types.—Holotype, allotype, and paratypes in CSIRO. Altogether 300 paratypes designated and series distributed to AM; BM; MACL; NM; SAM; NSWDA. Holotype ♂: "Black Mt., A.C.T., 31.1.1951, P. B. Carne". Allotype ♀: "Queanbeyan, N.S.W., P. B. and L. C. Carne, 30.12.1947". Paratypes: 5 ♀♀ from Queanbeyan, N.S.W., remainder from Canberra, taken either in light traps at Black Mountain, or on eucalypts in the vicinity. Dates of collection range from 26th December to 30th January, with the majority taken during the third week of January.

The trivial name is derived from an aboriginal word meaning "high ground".

13. ANOPLOGNATHUS CHLOROPYRUS (Drapiez)

Figs. 40, 41

Rutela chloropyra Drapiez, 1819, Ann. Sci. Phys. Bruxelles 2: 44, pl. 16, fig. 4.

Anoplognathus chloropyrus Blanchard, 1850, Cat. Coll. Ent. Col. p. 222; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin, ent. Ztg 65: 94.

Anoplognathus nitidulus Boisduval, 1835, Voy. Astrolabe, Col. 2: 176.

Anoplognathus chloropygus Ohaus, 1918, Col. Cat. Junk 20: 170.

The incorrect spelling "chloropygus" given by Ohaus in his catalogue has been perpetuated in most identifications made since its publication.

The species is very distinct, being immediately recognized by its strikingly bright green pygidium. It is very abundant in parts of its range and is often responsible for severe defoliation of eucalypts.

Yellowish brown or medium biscuit with green or reddish golden reflections on the head, pronotum, scutellum, and legs. Abdomen and thorax deep green and with white villosoity, the former tending to be glabrous along mid line; fore coxae, tarsi, and mouthparts almost black, with a green sheen.

♂. Length 19–23 mm. Clypeus glabrous, sides convex in dorsal profile, anterior margin recurved, truncated face lightly setose; clypeofrontal suture transverse, green. Head with dense fine punctures and micropunctures; ocular canthi bearing pale brown setae.

Pronotum with sides evenly rounded, anterior angles acute, basal margin bisinuate with the ridge widely obsolete across middle; anterior margin with a median node, disc with fine sparse punctures, a weakly median line, and with slight lateral compressions of surface. Scutellum lightly punctate.

Elytra with white humeral hairs, epipleurae with white hairs and serrations near apices, the latter contiguous and squarely cut, surface almost vertical below subapical calli; median sutures stained greenish brown, sutural striae impressed

just at apices, disc with distinct punctate striae, the punctures deeply impressed; micropunctures present.

Fore tibiae broad, with short white hairs, strongly 3-dentate. Hind legs slender, sparsely clothed, tibial spurs separated by 2-3 fine ciliae; tarsi elongate.

Mesosternal process flat, not depressed, tapering abruptly to slender acute apex overhanging hind margin of fore coxae.

Propygidium with white caudal fringe; pygidium uniformly rugulose, brilliant green, with very sparse short white hairs and abundant long pale brown hairs behind and on apical ridge, the disc weakly convex in profile, sometimes compressed laterally and in extreme angles. Abdomen with abundant rather long white hairs. Genitalia as in Figures 40, 41.

♀. Length 21-26 mm. Clypeus transverse, anterior margin gently recurved; elytra distinctly flared at level of hind coxae, apices with brushes of fine brown hairs. Fore tibiae strongly 3-dentate, tarsi with larger claws (usually) toothed. Apical ridge of pygidium obsolete in middle, disc almost flat. Last abdominal sternite setose. Antennal club equal in length to that of male.

Very occasionally the pygidium possesses a greenish rose sheen. Its degree of convexity in the male is variable; individuals are found in which the sclerite is highly convex.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—QUEENSLAND: Nambour, Southport, Stanthorpe, Yandilla. NEW SOUTH WALES: Armidale, Barrington Tops, Bathurst, Berrima, Blue Mountains, Braidwood, Canberra (A.C.T.), Cullerin, Exeter, Glenfield, Glen Innes, Gloucester, Kangaroo Valley, Kincumber, Mittagong, Nerriga, Penrith, Richmond, Snowy R., Sydney, Taralga, Tenterfield, Wollongong. VICTORIA: Lakes Entrance, Leongatha, Sale, Wonnongatta.

Dates of collection.—November to January.

Specimens examined.—Approx. 500.

14. *ANOPLOGNATHUS BOISDUVALI* Boisduval

Figs. 42, 43

Anoplognathus boisduvali Boisduval, 1835, Voy. Astrolabe, Col. 2: 171; Macleay, 1873,

Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 97.

Anoplognathus pulchripes Burmeister, 1844, Handb. Ent. 4 (1): 444.

Anoplognathus lineatus Macleay, 1864-5, Trans. Ent. Soc. N.S.W. 1 (Proc.): xix.

This is a quite distinct although somewhat variable species; superficially it may be confused with the more heavily pigmented examples of *porosus* (Dalm.). The lighter coloured forms are found in the drier parts of the range of the insect, e.g. Trangie, N.S.W.

Light biscuit to yellowish brown forms, with elytral striae deeply pigmented, the whole (especially the head and pronotum) with greenish golden reflections; underside reddish brown changing to green at sides of the sternites; femora with greenish sheen, tibiae rose. Abdomen with abundant white hairs except on last segment, not continuous across middle; hind tarsi almost black.

♂. Length 21–24.5 mm. Clypeus with sides straight, converging towards recurved anterior margin; apical truncated face lightly setose, suffused with deep brown at edge. Head glabrous, with very dense fine punctures, these becoming sub-confluent on ocular margins of frons; clypeofrontal suture brown, slightly curved anteriorly. Ocular canthi bearing white setae.

Pronotum with sides subparallel near base, contracted behind acute and somewhat produced anterior angles; margins golden or greenish brown, the basal margin strongly bisinuate and with the ridge widely obsolete across middle; disc with very fine punctures, surface finely rugulose near lateral margins, without trace of a median line. Scutellum impunctate.

Elytra with humeral angles and epipleurae glabrous, the latter strongly serrate near apices and slightly flared below humeral calli; the disc compressed below and behind the latter, bearing fine punctures underlain by deeply pigmented spots of varying continuity, surface weakly microreticulate, subapical calli denticulate; apices individually rounded and giving rise to a very small re-entrant angle.

Fore tibiae bearing white hairs, moderately broad, 3-dentate but with basal tooth small. Hind legs slender, femora almost glabrous, tibiae with very sparse white hairs, spurs separated with 2 stout ciliae.

Mesosternal process glabrous, slightly depressed and recurved towards bluntly rounded apex; the latter overhanging fore coxae. No postcoxal prosternal process.

Propygidium with conspicuous caudal fringe of white hairs; pygidium weakly convex in profile, finely and evenly rugulose, uniformly clothed with very short white hairs (sometimes lacking) and with sparse longer brown hairs at apex; sides slightly compressed, apical ridge fine and continuous, disc with greenish reflections. Abdominal sternites with rather scale-like decumbent white hairs. Genitalia as in Figures 42, 43.

♀. Length 20–27.5 mm. Antennal club distinctly shorter; clypeal margin scarcely more elevated anteriorly than at sides, whole head closely and heavily punctate; larger fore tarsal claws toothed; elytra with weak humeral setae; pygidium setose at lateral angles only; last abdominal sternite setose across middle.

Pygidium usually with greenish violet reflections but sometimes a brilliant green, especially in the darker individuals.

Type localities.—*lineatus*: Port Denison, Qld. Others unknown.

Type locations.—Unknown.

Distribution.—QUEENSLAND: Ayr, Babinda, Beaudesert, Benarkin, Biloela, Brisbane, Bulimba, Bundaberg, Byfield, Cairns, Charter's Towers, Cooktown, Cordalba, Deeral, Farleigh, Gatton, Gin Gin, Gordonvale, Herberton, Innisfail, Kuranda, Lawes, Lolworth, Mackay, Nambour, Pialba, Pittsworth, Port Denison, Rockhampton, Rosedale, Sarina, Stanthorpe, Warwick. NEW SOUTH WALES: Narromine, Sydney, Taree, Trangie.

Dates of collection.—October to April.

Specimens examined.—27 ♂♂, 42 ♀♀.

15. ANOPLOGNATHUS PRASINUS (Laporte)

Figs. 44, 45

Paranonca prasina Laporte, 1840, Hist. Nat. Col. 2: 143.

Anoplognathus prasinus Lansberge, 1873, Ann. Soc. Ent. Belge 16 (C.R.): 86; Ohaus, 1898, Stettin. ent. Ztg 59: 31; 1904, op. cit. 65: 98; Lea, 1919, Trans. Roy. Soc. S. Aust. 43: 241.

This species was described by Laporte who erected the monotypic genus *Paranonca* to receive it. It was transferred to *Anoplognathus* on the suggestion of Lansberge (1873), supported by Ohaus (1904) who redescribed it; Lea (1919) referred to examples in the South Australian Museum and published a photograph of a specimen. The author has seen the latter, and several other specimens. The species is often incorrectly identified as a *Paraschizognathus*.

Apple green, with margins of head, clypeofrontal suture, and anterior and posterior margins of pronotum translucent reddish yellow. Posterior half of epipleurae opaque brownish yellow, this light pigment extending on to surface of elytra as a band widening to maximum beneath subapical calli, then contracting slightly towards apices; sutural intervals, bases of elytra, and apex of mesosternal process similarly pigmented. Mouthparts brownish yellow, coxae and legs yellowish green, tarsi reddish brown, abdomen deep brownish green.

♂. Length 18–20 mm. Antennal club equal in length to shaft, Clypeus of the *porosus* type, sides strongly convergent, truncate, anterior angles rounded, sides barely raised, anteriorly abruptly curved, truncated face short and bearing white hairs, as also ocular canthi; disc glabrous, with fine punctures and micro-punctures; clypeofrontal suture transverse.

Pronotum transverse, widest near obtuse basal angles, anterior angles subacute, anterior and basal ridges almost or quite continuous, the latter evenly rounded, not bilobed; disc finely punctate, with a vague median impunctate stripe. Scutellum glabrous, finely punctate.

Elytra with epipleurae well defined, not flared, serrate near apices, bearing sparse white hairs and a narrow membranous border; disc with well-defined rows of rather heavily impressed punctures, humeral calli barely discernible, subapical calli ridge-like, apices contiguous and squarely cut.

Fore tibiae 3-dentate, median tooth closer to distal than to proximal tooth, the latter very small.

Mesosternal process flat, sharp, setose, extending to mid point of fore coxae. Hind legs very slender, tibial spurs acute, separated by 2 fine ciliae.

Abdominal sternites with sparse decumbent white hairs across middle; pygidium slightly convex in profile, compressed at sides, confluently punctate, bearing short decumbent white hairs on disc, and long erect brownish yellow setae near margins. Genitalia as in Figures 44, 45.

♀. Length 21–22 mm. Clypeus rounded, margins scarcely recurved. Antennal club shorter than shaft. Pronotum with pair of distinct paramedian impressions. Larger fore tarsal claws toothed. Pygidium flat.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—QUEENSLAND: Caloundra, Cudlo, Cunundi, Gympie, Montville, Tambourine. NEW SOUTH WALES: Richmond R.

Dates of collection.—November to January.

Specimens examined.—9 ♂♂, 5 ♀♀.

Collections.—CSIRO; MACL; QDAS; QM; QU; SAM.

16. ANOPLOGNATHUS MULTISERIATUS Lea

Anoplognathus multiseriatus Lon., 1919, Trans. Roy. Soc. S. Aust. **43**: 241, pl. 25, fig. 36; pl. 27, fig. 67.

The following notes are additive to Lea's description, which was based on a unique female from Bribie I., Qld.

Dorsal surface with green sometimes diluted with a dull red-brown. ♂ with clypeus highly transverse, sides strongly convex in dorsal profile, anteriorly with a broad strongly recurved margin, the anterior truncated face lightly setose. Clypeofrontal suture transverse; ocular canthi bearing white hairs.

Elytra with epipleurae thickened over junction of middle and hind coxae, weakly serrate near apices, the latter contiguous and squarely cut. Subapical calli poorly developed in ♀, slightly denticulate in ♂. Hind legs moderately stout, tibiae with distinct median carinae bearing stout black ciliae; spurs separated by 3 ciliae in ♀, 2 in ♂. Mesosternal process slightly depressed, setose on mid line to level of mesocoxae, its apex acute and overhanging mid fore coxae.

Pygidium slightly convex in lateral profile, the angles impressed in ♀, the sides compressed in ♂; apex subtruncate.

Type locality.—Bribie I., Qld.

Type location.—QM.

Plesioallotype ♂: "Uki, Tweed Riv., 30 Oct. 1922. Taken on leaves of *Banksia serrata*, C. Deuquet" (CSIRO, presented by collector, designated by present author).

Specimens examined.—"1 ♀, type, Bribie I. C/2091; 1 ♂, Bribie I. 16.11.19, P. Frenzen"; 1 ♂, "Gordouvalo, W. C. Dormor" (QM). 1 ♀, "Queensland" (NM). 1 ♀, "Uki, Tweed R., C.D." (Deuquet Coll.).

17. ANOPLOGNATHUS PALLIDICOLLIS Blanchard

Figs. 46–50

Anoplognathus pallidicollis Blanchard, 1850, Cat. Coll. Ent. Col., p. 222; Macleay, 1873, Trans. Ent. Soc. N.S.W. **2**: 355; Ohaus, 1904, Stettin. ent. Ztg **65**: 100.

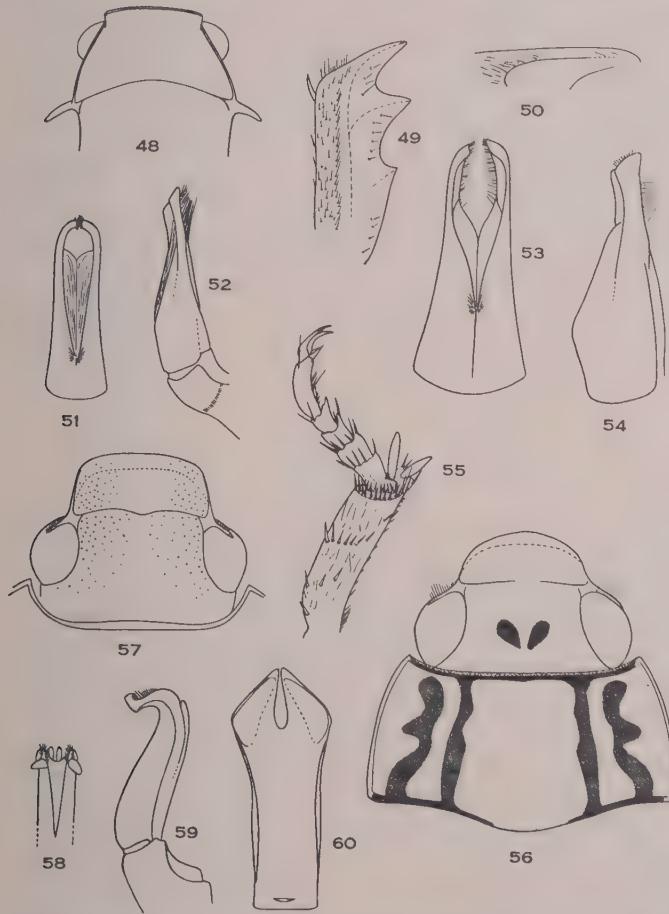
Macleay (1873) regarded this as a form of the highly variable species *porosus* (Dalm.), but Ohaus (1904) correctly recognized it as an independent species. It is distinguishable by the form of its mesosternal process and by the vestiture of its pygidium.

Pale biscuit to medium yellowish brown, rather glossy, with very little coloured sheen except for a weak rose on pygidium and a faint greenish gold on margins of pronotum and scutellum. Abdomen and thorax very dark green or black.

♂. Length 18–23 mm. Clypeus (Fig. 48) with sides almost straight, converging towards abruptly recurved anterior margin; truncated face short, setose. Head glabrous, slightly coppery; clypeus smooth, finely punctate; frons more coarsely so; clypeofrontal suture reddish brown, curved anteriorly, strongly pigmented at sides. Ocular canthi bearing white setae.

Pronotum widest at basal angles, anterior angles subacute, not produced, ridges narrowly obsolete across middle; disc finely and sparsely punctate, with a weakly impressed median line and with paired antero- and basolateral impressions; the basal margin bisinuate.

Elytra finely punctate, each puncture underlain by a small pigmented spot; epipleurae glabrous, very slightly dilated above mesocoxae, serrate near apices; the latter contiguous or almost so (giving rise to a very small acute re-entrant angle).



Figs. 48–50.—*A. pallidicollis* Blanch.: 48, ♂ head, dorsal; 49, ♂ right fore tibiae, dorsal; 50, ♂ mesosternal process, lateral. Figs. 51, 52.—*A. concolor* Burm.: 51, gonostyli, dorsal; 52, gonostyli, lateral. Figs. 53–56.—*A. abnormis* Macl.: 53, gonostyli, dorsal; 54, gonostyli, lateral; 55, ♀ hind tibiae and tarsus, dorsal; 56, ♂ head and pronotum, dorsal. 57.—*A. rothschildii* Ohaus: ♂ head, dorsal. Figs. 58, 59.—*A. aureus* Waterh.: 58, gonostylar apices, dorsal; 59, gonostyli, lateral. Fig. 60.—*A. punctulatus punctulatus* Oll.: gonostyli, dorsal.

Fore tibiae (Fig. 49) abundantly clothed with white hairs, acutely 3-dentate; hind legs slender, tibiae bearing both white hairs and dark ciliae; the spurs separated by 2 fine ciliae.

Mesosternal process (Fig. 50) very long, flat, setose at sides, tapering to a slender apex overhanging fore coxae. No postcoxal process present. Abdomen with decumbent white hairs, subobsolete on mid line except on last sternite.

Pygidium nearly flat in profile, uniformly clothed with white hairs and with short brown hairs on and near continuous apical ridge. Genitalia as in Figures 46, 47.

♀. Length 20–24 mm. Head more densely and finely punctate, not strongly emarginate anteriorly; epipleurae contracted at sides, with slight dilation as in male. Larger fore tarsal claws toothed. Pygidium almost concave in profile. Abdominal sternites clothed nearer to mid line.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—QUEENSLAND: Belmont, Bribie I., Brisbane, Bundaberg, Cairns, Croftby, Innisfail, Mackay, Nambour, Pialba, Rosedale, Sandgate, Stanthorpe. NEW SOUTH WALES: Bathurst, Caldwell, Canberra (A.C.T.), Corowa, Forbes, Grenfell, Inverell, Queanbeyan, Sydney, Tenterfield, Trangie, Tweed R., Wallendbeen. VICTORIA: Ararat, Bacchus Marsh, Dimboola, Inglewood, Mansfield, Melbourne, Mooney's Gap, Mooroopna, Murray R., Ouyen, Rutherglen, Tallarook.

Dates of collection.—October to January. This species is very abundant in Canberra where peak flights occur from late December to early January.

Specimens examined.—Approx. 200.

18. ANOPLOGNATHUS CONCOLOR Burmeister

Figs. 51, 52

Anoplognathus concolor Burmeister, 1855, Handb. Ent. 4 (2): 524; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus. 1904, Stettin. Ent. Ztg 65: 99.

This small, rather drab species has been confused with *pallidicollis* in many collections; it is readily distinguishable from this species by the form of its clypeus in the male and by the peculiar appearance of its elytra.

Light biscuit coloured, with pigment lacking over much of elytral disc giving a water-soaked appearance. Clypeal and pronotal margins stained a dark brown. Underside reddish yellow to reddish brown; mesosternum a deep brownish black.

♂. Length 15.5–18 mm. Clypeus subrectangular, angles rounded, weakly and evenly emarginate; whole head closely but shallowly punctate, clypeofrontal suture transverse, most strongly pigmented at sides; ocular canthi bearing white setae.

Pronotum with sides rounded, anterior angles blunt, basal margin with a single lobe, the ridge only just obsolete across the middle; disc sparsely and finely punctate, lacking or with only a very faint median stripe.

Elytra with epipleurae glabrous, weakly serrate near apices; the latter contiguous but not quite squarely cut; disc with fine punctuation, somewhat flattened in middle and compressed below humeral calli.

Fore tibiae bearing light brown hairs, bidentate, the apical teeth prolonged, tarsi with 1st segments elongate. Hind legs rather stout, femora clothed, tibiae heavily punctate and bearing both stout ciliae and white hairs; spurs separated by 2 stout ciliae.

Mesosternal process flat, slender, with sparse white hairs in region of mesocoxae, apex sharply rounded, overhanging fore coxae; no postcoxal process discernible. Abdomen with sternites conspicuously punctate, bearing short pale yellowish brown

dark and white intermixed rather elongate scales, sparse across midline except on last sternite.

Pygidium densely covered with short decumbent white hairs and with longer fine brown hairs at apex, the apical ridge smooth; the disc flat in lateral profile. Genitalia as in Figures 51, 52.

♂ Length 13-20 mm. Antennal club slightly shorter than in ♂; elytra less rectangular, few elongate appressed surface strongly microgranular. Fore tibiae distinctly 3-dentate, the distal teeth few elongate claws simple.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—Australia. Belmont, Brabene, Brookfield, Burra Mt., Dargaville, Gippsland, Latrobe, N. Pines Mts., near south walla, Blue Mountains, Clarence R., Dorrigo, National Park, Newport, Sydney, Tweed R.

Date of collection.—November to March.

Specimens examined.—8 ♂♂, 14 ♀♀.

Collections.—CSIRO; NM; QDAS; QM; QU.

19. *ANOPLOGNATHUS ABNORMALIS* Macleay

Figs. 53-56

Anoplognathus abnormis Macleay, 1858, Trans. Ent. Soc. N. S. W. 2: 359; Chama, 1864.

Sectim. ent. Zag 65: 67, 108.

Anoplognathus quadrioculata Waterhouse, 1874, Trans. Ent. Soc. Lond. 1874: 533.

Yellowish brown with longitudinal dark brown to black markings on vertex, pronotum, margins of scutellum and bases of elytra (Fig. 56); legs darker, abdomen almost reddish brown and marked with white hairs except on midline. Elytra with creamy zones adjacent to margins and patches of similar texture near scutellum.

♂ Length 13-14.5 mm. Elytra transverse wider parallel near base, evenly rounded anteriorly, anterior margin moderately, the sides slightly recurved, disc with shallow surface punctures, these becoming confluent near margin, apical transverse face short and sparsely setose. Olfactory setae slightly curved anteriorly, suborbital or subdiscal surface middle apparently pigmented at sides. Ocular carina bearing white setae. Eyes protuberant.

Pronotum with sides evenly rounded, anterior angles acute, anterior ridge with a slight median node, posterior margin weakly transverse, the ridge obsolete across the middle, disc moderately and evenly punctate except on narrow median stripe.

Elytra with humeral angles gibbose, the surfaces brown, epipleurae weakly convex and serrate towards spine, sterna elongate and slightly notched.

Fore tibiae bearing inconspicuous white hairs, 3-dentate but with the basal tooth incomplete save with last segment elongate. Hind tibiae (Fig. 55) punctate bearing both dark villosa and white hair, spurs separated by several strong oblique lines, the tarsi elongate.

Mesosternal process gibbose, depressed but not recurved at apex, the latter narrowly rounded and overhanging fore tibiae. No postmarginal process discernible.

Pygidium densely and evenly clothed with decumbent white hairs and with sparse longer pale brown hairs near apical ridge, the disc flat in profile. Genitalia as in Figures 53, 54.

♀. Length 13–17 mm. Antennal club distinctly shorter; eyes less protuberant; clypeus with margins less recurved, evenly rounded from base, the disc confluent punctate. Fore tibiae more acutely 3-dentate and with basal tooth distinct, claws simple; elytra with apices slightly rounded, sometimes not quite contiguous and giving rise to a deep but very narrow re-entrant angle.

Type locality.—Wide Bay, Qld.

Types.—♂ holotype and ♀ allotype selected from type series in MACL.

Distribution.—QUEENSLAND: Cairns, Innisfail, Mackay, Wide Bay.

Dates of collection.—December.

Specimens examined.—9 ♂♂, 11 ♀♀.

Collections.—BSES; CSIRO; MACL; NM; QDAS; QM; QU.

20. ANOPLOGNATHUS ROTHSCILDITI Ohaus

Fig. 57

Anoplognathus rothschildti Ohaus, 1898, Stettin. ent. Ztg 59: 35; op. cit. 65: 109.

A small, apparently uncommon species with the eyes unusually protuberant in the male.

Reddish brown or reddish yellow; pronotum, scutellum, and elytra with deep greenish brown margins, clypeus with margin dark; clypeofrontal suture darkened at sides. Head and thorax with greenish golden reflections; mesosternum greenish; abdomen chestnut; legs reddish brown with greenish sheen; tarsi black with green sheen. Elytra with light zone about margins, especially noticeable in the female.

♀. Length 15–18 mm. Clypeus transverse, sides slightly convergent, anterior angles rounded, with slight but regular emargination, with very short, setose, anterior truncated face, disc densely punctate, frons more sparsely so; clypeofrontal suture continuous, slightly curved anteriorly and with a median posterior node. Ocular canthi bearing white setae.

Pronotum highly transverse, sides subparallel at base then rounded to anterior angles, the latter neither produced nor acute; basal margin very slightly lobed, not bisinuate, the ridge obsolete across the middle.

Elytra glabrous at humeral angles, epipleurae sparsely setose near apices, non-serrate, slightly flared above hind coxae, apices contiguous, almost squarely cut; disc with punctures lightly impressed, sutural striae linear in apical third.

Fore tibiae with basal tooth subobsolete, apical tooth prolonged; anterior claws not toothed; hind tibial spurs separated by 2 long slender ciliae.

Mesosternal process very slightly depressed, glabrous, apex narrowly rounded, overhanging fore coxae. Abdominal sternites with sparse white hairs in single row across middle, more numerous at sides. Pygidium flat, with uniform clothing of decumbent white hairs; apical margin obsolete in middle, disc with green reflections.

♂. Length 14·5–16 mm. Clypeus (Fig. 57) with strongly reflexed anterior margin, but continuous with lateral margins, the sides more nearly parallel than in ♀; disc with punctuation reduced on mid line, sparser and generally finer; clypeofrontal suture quite transverse, but with posterior node in middle. Elytra with epipleurae weakly serrate, apices cut squarely but not contiguously, giving rise to a long, deep re-entrant angle. Fore tibiae with basal tooth quite obsolete, apical tooth not produced. Hind tibial spurs separated by weaker ciliae. Pygidium slightly convex in profile, apical ridge not obsolete across middle. Eyes markedly protuberant.

Type locality.—Geraldton (= Innisfail), Qld.

Type location.—Rothschild Coll., Tring Museum (according to Ohaus).

Distribution.—QUEENSLAND: Babinda, Innisfail, Kuranda. WESTERN AUSTRALIA: Albany-Caligan R.*

Specimens examined.—2 ♂♂, 1 ♀

Collections.—BM; CSIRO; SAM.

21. ANOPLOGNATHUS AUREUS Waterhouse

Figs. 58, 59

Anoplognathus aureus Waterhouse, 1889, Ann. Mag. Nat. Hist. (4) 3: 360; Ohaus, 1904, Stettin. ent. Ztg 65: 92.

Calloodes frenchi Blackburn, 1890, Proc. Linn. Soc. N.S.W. (2) 5: 148.

Anoplognathus concinnus Blackburn, 1900, Trans. Roy. Soc. S. Aust. 26: 40; Ohaus, 1904, Stettin. ent. Ztg 65: 91; Arrow, 1919, Ann. Mag. Nat. Hist. (9) 4: 379.

Considerable confusion has been caused by Blackburn's placement of this species in *Calloodes*, to which genus it does not belong. It is often identified as *C. frenchi* Ohaus, a quite distinct species correctly referred to that genus. Blackburn's other name, *concinnus*, refers to specimens which are merely colour variants of *aureus*. Arrow (1919) pointed out that intermediates between the two forms occur. It is interesting to note that an exactly comparable variant occurs in the other golden species of *Anoplognathus*—*parvulus* Waterhouse—but this has escaped being given a separate name.

Ranging from pure golden to glossy reddish brown, with intermediates in which the two colours occur, appearing as if the gold had been abraded to expose an underlying reddish brown pigment. Legs reddish brown.

♂. Length 12·5–14·0 mm. Clypeus narrowing from base towards apex, then dilated at sides of strongly recurved anterior margin; apical truncated face sparsely setose; disc glabrous, shining, with sparse shallow punctures. Clypeofrontal suture transverse, fine, and dark. Ocular canthi bearing short white setae.

Pronotum with sides scarcely rounded, subangulate near middle, anterior angles acute and sometimes produced, anterior and basal margins with ridges widely obsolete across middle, the latter bisinuate; disc impunctate except adjacent to lateral ridges. Scutellum smooth, the edges stained violet-magenta.

* This record based on a ♂ in the British Museum (Fry Coll. 71849) and determined by Ohaus.

Elytra impunctate or with faint striae of subobsolete punctures near lateral margins; epipleurae serrate near apices, the latter contiguous but not quite squarely cut.

Fore tibiae with sparse pale brown hairs, 2- or 3-dentate, distal teeth acute, and at wide angle to major axis of tibiae. Hind tibiae distinctly bicarinate, spurs separated by 2 fine ciliae.

Mesosternal process flat, glabrous, tapering to acute apex overhanging hind margin of fore coxae. Postcoxal process present. Thoracic vestiture sparse.

Propygidium with narrow brown caudal margin; pygidium very slightly convex in profile, impunctate except for sparse short white hairs and longer pale brown hairs on apical ridge. Abdominal sternites brown on their posterior margins; the abdomen and mesosternum always with some golden sheen even in extreme *concininus* variants. Genitalia as in Figures 58, 59.

♀. Length 14.5–16.5 mm. Clypeus rather rounded, evenly emarginate, with punctuation closer and more heavily impressed. Fore tibiae with distinct basal teeth, tarsi with the larger claws toothed. Usually the fore tibial teeth are more elongate than in the ♂ and lie at a smaller angle to the major axis of the tibia.

Type localities.—*aureus*: Queensland; *frenchi* and *concininus*: North Queensland.

Type locations.—*aureus*, *frenchi*, and *concininus* in BM.

Distribution.—QUEENSLAND: Babinda, Cairns, Daintree, Innisfail, Johnston R., Mackay, Mossman.

Dates of collection.—November to February.

Specimens examined.—Typical *aureus*: 19 ♂♂, 9 ♀♀ (including cotype of *frenchi*); typical *concininus*: 8 ♂♂, 1 ♀; intermediates: 2 ♂♂, 1 ♀.

Collections.—BM; BSES; CSIRO; MACL; NM; SAM; QDAS; QM; QU.

22a. ANOPLOGNATHUS PUNCTULATUS PUNCTULATUS Olliff

Fig. 60

Anoplognathus punctulatus Olliff, 1890–91, Rec. Aust. Mus. 1: 72, pl. 10, fig. 8; Ohaus, 1898, Stettin. ent. Ztg 59: 33; 1904, op. cit. 65: 106.

A quite distinct large green species with a clypeus of the *brunnipennis* type and male genitalia of unusual shape.

Dorsally pure dark green but with distal portion of clypeus and margins of pronotum and scutellum stained with brown. Underside reddish brown with rose or green sheen; tarsi black with a coppery sheen.

♂. Length 19–23.5 mm. Clypeus with sides strongly concave in dorsal profile, the apex dilated and abruptly recurved; apical truncated face deep and glabrous; disc with dense short erect white hairs, the surface depressed at the sides and in middle behind anterior elevation, closely and almost confluent punctate; clypeofrontal suture slightly curved anteriorly; frons glabrous, with punctuation similar to that of clypeus.

Pronotum with sides evenly rounded, anterior angles produced and acute, anterior and basal margins with ridges obsolete, the latter bisinuate; disc regularly and thickly punctate, with faint narrow almost impunctate median line; micro-punctures present.

Elytra with white hairs at humeral angles; epipleurae with abundant white hairs and slight serrations near apices, the latter contiguous and squarely cut; disc with dense fine punctures becoming confluent near lateral and apical margins.

Fore tibiae weakly bidentate, or with a vague basal tooth in addition, surface microreticulate, bearing abundant white hairs; tarsi very short and cylindrical.

Hind legs with white hairs, tibial spurs separated by 2 fine ciliae, femora setose only on anterior margins. Tarsi exceptionally short and stout.

Mesosternal process conspicuous, strongly curved and reflexed at narrowly rounded apex, the latter overhanging fore coxae, quite glabrous, brownish black and with a green sheen. No postcoxal process present. Abdomen with abundant white hairs at sides of sternites, sparse across mid line.

Pygidium coppery, with dense clothing of decumbent white hairs; with similar hairs on caudal margin of propygidium. Disc of pygidium flat, apical ridge obsolete in middle, bearing erect yellowish hairs. Genitalia as in Figure 60.

♀. Length 20.5–24 mm. Clypeus glabrous, rounded, slightly and evenly emarginate; fore tibiae 3-dentate, tarsi with 1st segments very long, larger claws toothed. Hind tibial spurs separated by 2 stout ciliae. Pygidium similar to that of ♂.

Type locality.—Mt. Bellenden-Kerr, Qld.

Type location.—Unknown.

Distribution.—QUEENSLAND: Ayr, Byfield, Cairns, Daintree, Deeral, Gordonvale, Innisfail, Jaffa, Kuranda, Mackay, Malanda, Meringa, Mossman, Redlynch, Ravenshoe, Tully, Yoffa.

Dates of collection.—November to March.

Specimens examined.—26 ♂♂, 22 ♀♀.

Collections.—AM; BSES; CSIRO; MACL; NM; QDAS; QM; QU.

22b. ANOPLOGNATHUS PUNCTULATUS INSULARIS Ohaus, stat. nov.

Figs. 61–63

Anoplognathus insularis Ohaus, 1898, Stettin. ent. Ztg 59: 33; 1904, op. cit. 65: 107.

Ohaus (1904) says "This species is obviously closely related to *punctulatus*, being possibly only a local race with weaker sculpturing and more hair; however, among approximately 200 *punctulatus* specimens I have not found a single one with even a suspicion of coppery colour on the upper surface."

The author considers that the differences are greater than would be expected in a "local race" and treats it as a subspecies of *punctulatus*. From the latter it differs as follows:

Dorsal surface bronze or green with a bronze sheen; anterior truncated face of clypeus weakly setose, disc less closely punctate, clypeofrontal suture weakly sinuate (Fig. 61). Pronotum with anterior angles more produced, rather acute. Elytral punctuation far less pronounced, micropunctate only on most of disc; hind tibiae with single stout ciliae between spurs. Pygidium more abundantly clothed. Abdominal sternites with white hairs abundant nearer to mid line. Specimen examined has an aborted mesosternal process. ♂ genitalia as in Figures 62, 63. Fore tibiae distinctly 3-sinuate.

Length of male 21–23 mm; female 22 mm.

Type locality.—Mt. Alexander—Mt. Nisbet, British New Guinea.

Type location.—In Ohaus Collection.

Distribution.—New Guinea.

Specimens examined.—1 ♂, “New Guinea, Pratt. B.M. 1932–116, det. Arrow from descr.” (BM).

23. ANOPLOGNATHUS SMARAGDINUS Ohaus

Figs. 64, 65

Anoplognathus smaragdinus Ohaus, 1904, Stettin. ent. Ztg 65: 90.

Calloodes prasinus Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 359 (nom. praeocc.).

Calloodes translucidus Benderitter, 1923, Bull. Soc. Ent. Fr., 1923: 93; 1924, op. cit. 1924: 137.

When Ohaus transferred *Paranonca prasina* Laporte to *Anoplognathus* it became necessary to change the name of the later-described species *prasina* MacL., and *smaragdinus* was selected. Benderitter described this species as *C. translucidus* in 1923, and realizing its prior description by Ohaus, suppressed the name in the following year.

The species is subject to colour variation; typical specimens are green but red, blue, and violet individuals are found.

Dorsal surface, mentum, mesosternum, and pygidium lacquer green, occasionally cherry red or bright blue; clypeus yellowish brown with a green sheen; legs, coxae, and abdomen yellowish brown with a golden green or coppery sheen.

♂. Length 15–19 mm. Clypeus with sides convex in dorsal profile, emarginate, then slightly depressed behind abruptly reflexed anterior margin, with a short glabrous truncated face. Head sparsely micropunctate, microreticulate; clypeofrontal suture transverse, deep green. Ocular canthi almost glabrous.

Pronotum and scutellum micropunctate, anterior angles acute, basal ridge continuous or just obsolete in middle, the margin bisinuate. Lacking a median stripe.

Elytra glabrous, epipleurae strongly serrate near apices, bearing minute hairs, slightly thickened above junction of meso- and metacoxae, apices contiguous, more or less squarely cut; disc finely punctate, apical calli strongly developed, weakly dentate on hind margins.

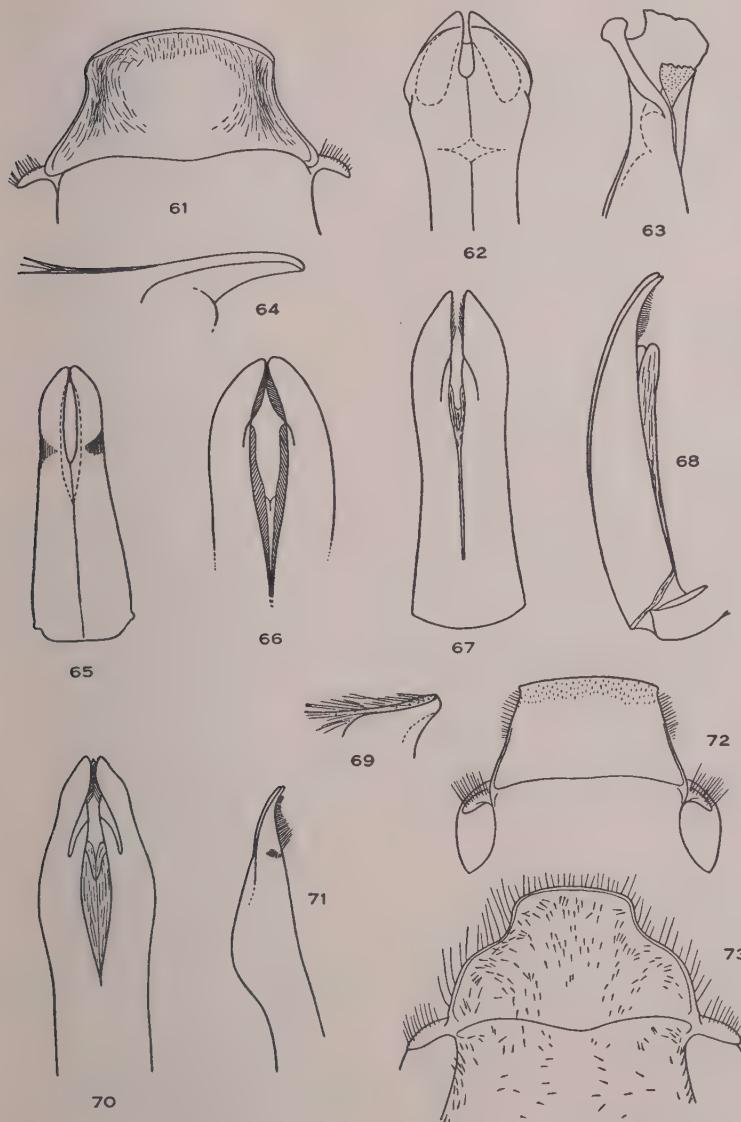
Fore tibiae with basal tooth subobsolete, surface almost glabrous. Hind legs slender, glabrous; tibial spurs separated by 2 fine ciliae.

Mesosternal process (Fig. 64) green, glabrous, depressed and recurved at apex, the latter pointed and overhanging fore coxae. Coxae and thoracic sternites with abundant hairs; abdomen almost glabrous except at lateral margins.

Pygidium flat or weakly convex in profile, glabrous except just behind fine continuous apical margin and for very short white hairs near the weakly impressed lateral angles; disc with shallow transverse punctures. Genitalia as in Figure 65.

♀. Length 18–21 mm. Clypeus semicircular, margin scarcely elevated. Fore tibial teeth 3-dentate, 1st tarsal segment very long, larger anterior claws toothed.

Type locality.—“N. Aust.”



Figs. 61–63.—*A. punctulatus insularis* Ohaus, stat. nov.: 61, ♂ head, dorsal; 62, gonostylar apices, dorsal; 63, gonostylar apices, lateral. Figs. 64, 65.—*A. smaragdinus* Ohaus: 64, ♂ mesosternal process, lateral; 65, gonostyli, dorsal. Fig. 66.—*A. aeneus* Waterh.: gonostylar apices, dorsal. Figs. 67, 68.—*A. suturalis* Boisd.: 67, gonostyli, dorsal; 68, gonostyli, lateral. Figs. 69–71.—Figs. 69, 71.—*A. hirsutus* Burm.: 69, ♂ mesosternal process, lateral; 70, gonostylar apices, dorsal; 71, gonostylar apices, lateral. Fig. 72.—*A. rubiginosus* Macl.: ♂ head, dorsal. Fig. 73.—*A. velutinus* Boisd.: ♂ head, dorsal.

Type location.—♂ holotype and ♀ allotype of *prasinus* labelled "N. Queensland" selected from type series in MACL.

Distribution.—QUEENSLAND: Babinda, Brisbane, Byfield, Cairns, Cleveland Bay, Deeral, Gordonvale, Herberton, Innisfail, Johnston R., Meringa, Northeate, Tully, Victoria Mill.

Dates of collection.—November to March.

Specimens examined.—Approx. 150.

24. ANOPLOGNATHUS AENEUS Waterhouse

Fig. 66

Anoplognathus aeneus Waterhouse, 1868, Ent. Mon. Mag. 5: 8; Ohaus, 1904, Stettin. ent. Ztg 65: 93.

This striking and apparently rare species was described from a single female.

Large deep metallic green species with conspicuous punctation on elytra and sides of pronotum, abdomen coppery green, legs deep rose.

♂. Length c. 30 mm. Clypeus transverse, sides subparallel in basal half, finely emarginate, contracted to abruptly recurved anterior margin, apical truncated face with sparse short golden hairs; disc depressed near anterior angles and in middle behind margin, surface closely and heavily punctate and with occasional micropunctures. Clypeofrontal suture fine, transverse, with a slight median posterior node. Frons with punctures slightly sparser than on clypeus, with a weak median impunctate ridge extending from clypeofrontal suture; vertex with a slight median fovea. Ocular canthi bearing white setae.

Pronotum with ridges well defined except across middle of both anterior and posterior margins, the latter weakly bisinuate; disc with faint impunctate median stripe, elsewhere with fine sparse punctures becoming coarser and denser towards lateral margins, there subconfluent and interspersed with numerous micropunctures.

Elytra with apices contiguous, squarely cut; ends of sutural intervals slightly spinose; humeral calli not conspicuous, basal angles bearing groups of short white hairs; epipleurae coppery, almost glabrous except near apices where a few hairs borne in weak serrations; sutural striae impressed only near apices; disc with numerous strongly impressed elliptical punctures interspersed with micropunctures, the surface wrinkled near the lateral margins.

Fore tibiae clothed with white hairs, 3-dentate, with the teeth confined to the distal portion of the tibia and with their axes at a small angle to that of the tibia as a whole. Hind legs slender, tibiate bearing sparse white hairs and stout dark ciliae, spurs separated by single ciliae.

Mesosternal process strongly depressed, recurved at apex, the latter rounded and overhanging fore coxae; glabrous except for sparse fine hairs behind mesocoxae.

Pygidium green, with well-defined marginal ridge, the disc flat, bearing short pale hairs mixed with longer more erect pale brown hairs near and on apical ridge; surface coarsely and irregularly punctate, rugose, and slightly compressed at sides. Abdomen coppery, with decumbent white hairs, these least numerous along mid line. Genitalia as in Figure 66.

2. The author has not seen a specimen of this sex. Ohaus (1904) notes that "the clypeus . . . is a short trapezoid with greatly rounded angles, more densely punctate and less glossy than in the male . . . elytra widening slightly above the hind coxae, the epipleurae slightly thickened, especially near the humeral calli . . . the inner claw of the front legs of the female is cloven".

Type locality.—Rockingham Bay, Qld.

Type localities.—2 type in BM. ♂ plesiotype (present designation) "Kuranda, ex. French coll." (NM).

Distribution.—QUEENSLAND: Cardwell, Herberton, Kuranda, Rockingham Bay.

Dates of collection.—None known.

Specimens examined.—1 ♂.

25. ANOPLOGNATHUS VELUTINUS Boisduval

Figs. 73-75

Anoplognathus velutinus Boisduval, 1835, Voy. Astrolabe, Col. 2: 181; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 109.

This rather isolated species shows no obvious relationship to any other species or species group in the genus, although it has a superficial similarity to *antiquus* Arr.

Concolorous brown species with surface abundantly clothed with adpressed white scales; elytra with a pair of black spots behind and slightly below humeral calli; also a lighter pair on pronotum, most conspicuous in the female.

♂. Length 21.5-25 mm. Clypeus (Fig. 73) finely emarginate, sides parallel to each other at base, strongly depressed, anterior margin abruptly elevated in middle, with a deep setose truncate face; anterior two-thirds of disc rugulose. Clypeofrontal suture subobsolete, trinotulate; frons sparsely and irregularly punctate; ocular canthi bearing dense white setae.

Pronotum with sides strongly curved, anterior angles rather obtuse, basal angles distinctly so; basal margin with a simple median lobe, the ridge widely obsolete; disc lightly and rather closely punctate, with a faint median impunctate stripe. Elytra with epipleurae glabrous, dilated over junction of meso- and metacoxae; non-serrate, apices contiguous, squarely cut, the sutures slightly produced, forming short, sharp, inconspicuous spinules.

Fore tibiae acutely 3-dentate, basal tooth small, bearing both hairs and scales; hind legs with very dense clothing of pale yellowish hairs and white scales, the tibiae bicarinate and with spurs separated by 2 fine ciliae. Whole ventral surface, except last sternite, densely clothed.

Mesosternal process flat or depressed but not recurved, surface setose, apex sharp, overhanging fore coxae; no postcoxal process present.

Pygidium flat or weakly convex in profile, finely rugulose, bearing scales directed toward mid line and sparse erect white hairs behind apical ridge; the latter concolorous, and trinotulate in middle. Genitalia as in Figures 74, 75.

♀. Length 21.5-26.5 mm. Clypeus with margins sinuate, only slightly elevated in front; head more heavily and closely punctate, almost glabrous except on ocular

margins of frons. Larger fore tarsal claws toothed; hind tibial spurs separated by 4-5 fine ciliae; last abdominal sternite setose.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—QUEENSLAND: Brisbane, Caloundra, Stanthorpe, Toowoomba. NEW SOUTH WALES: Bingara, 28 miles E.S.E. of Canberra (A.C.T.), Canterbury, Clovelly, Coonabarabran, Fairfield, Glenfield, Jervis Bay, Sydney, Wandong. VICTORIA: Camberwell, Caulfield, Hall's Gap, Heidelberg, Heyington, Studley Park, Wallan. Ohaus records the species from Port Denison, Qld., Lambton, N.S.W., and Mansfield, Vic.

Dates of collection.—September (S. Qld.) to January (N.S.W. and Vic.).

Specimens examined.—12 ♂♂, 8 ♀♀.

26. ANOPLOGNATHUS SUTURALIS Boisduval

Figs. 67, 68

Anoplognathus suturalis Boisduval, 1835, Voy. Astrolabe, Col. 2: 178, pl. 9, fig. 8; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 111.

A very abundant and widely distributed species found feeding on the leaves of a number of *Eucalyptus* species.

Light yellowish to reddish brown, with weak green sheen on elytra; head, pronotum, and scutellum darker, with more pronounced green, especially at margins; abdomen, coxae, and thoracic sternites black, with abundant and very long white hairs. Legs red to yellowish brown, densely clothed with long white hairs.

♂. Length 18-22 mm. Clypeus slightly tapered, with sides straight until slightly dilated at recurved apical margin; moderately deep sparsely setose truncated face. Head with erect white hairs, with coarse subconfluent punctation; clypeofrontal suture transverse, with a median node, and strongly pigmented at sides. Ocular canthi bearing white setae.

Pronotum weakly convex, sides parallel in basal half or evenly rounded, anterior angles subacute; anterior ridge continuous, basal ridge obsolete across middle, the margin weakly bisinuate; disc with fine punctuation becoming confluent rugulose at sides, bearing setae near anterior angles and with a median impunctate stripe. Margins of scutellum brown.

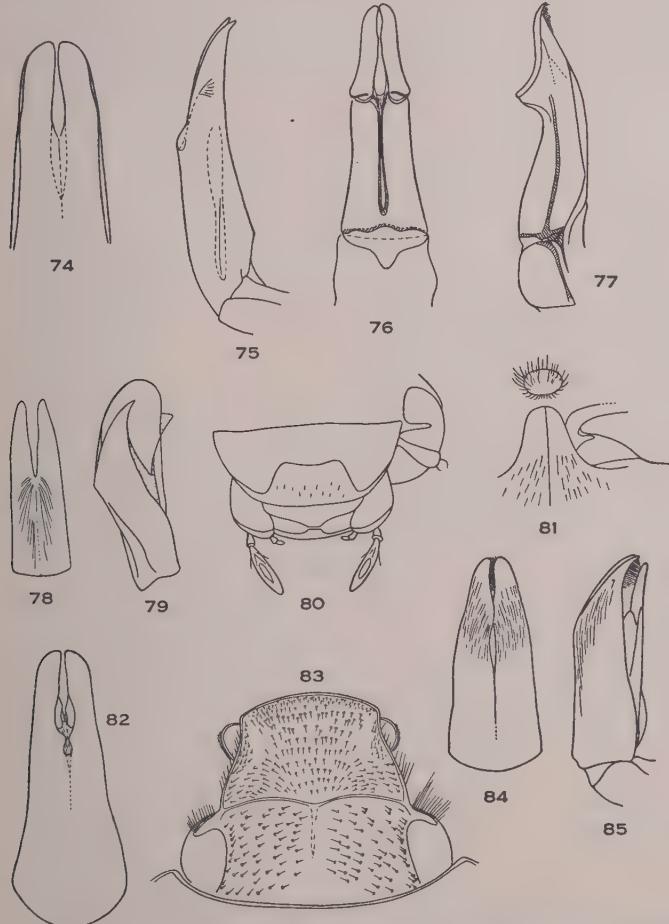
Elytra microreticulate, basal angles with white hairs, epipleurae with sparse hairs and obsolescent serrations near apices, the latter contiguous and more or less squarely cut; disc with fine punctuation, the sutures dark brown.

Fore tibiae broad, bearing abundant white hairs, 3-dentate, the teeth rather close together and at a wide angle to major axis of tibia; tarsi black. Other legs very hairy, hind tibiae without distinct carinae, spurs separated by 2 fine ciliae.

Mesosternal process black, setose, acutely pointed, the apex extending only half way to fore coxae. All abdominal sternites black, setose except on middle of last sternite.

Propygidium black; pygidium variably convex in profile (often strongly so), bright green or black with a coppery sheen, bearing long brown hairs on apical ridge, the disc with abundant erect white hairs, punctures shallow and distorted, micropunctures present. Genitalia as in Figures, 67, 68.

♀. Length 19–23 mm. Clypeus of normal ♀ type, more closely and finely punctate than in ♂, much less abundantly clothed. Pronotum almost or quite glabrous. Elytra with apices squarely cut, epipleurae widely flared over hind coxae. Fore tibiae narrower, the teeth more deeply cut; hind tibial spurs much shorter. Last abdominal sternite setose across middle; pygidium flat.



Figs. 74, 75.—*A. velutinus* Boisd.: 74, gonostylar apices, dorsal; 75, gonostyli, lateral. Figs. 76, 77.—*A. parvulus* Waterh.: 76, gonostyli, dorsal; 77, gonostyli, lateral. Figs. 78–81.—*A. daemeli* Ohaus: 78, gonostyli, dorsal; 79, gonostyli, lateral; 80, ♂ head, anterior; 81, ♂ mesosternal process and prosternal process, ventral. Figs. 82, 83.—*A. antiquus* Arr.: 82, gonostyli, dorsal; 83, ♂ head, dorsal. Figs. 84, 85.—*A. brunniipennis* Gyll.: 84, gonostyli, dorsal; 85, gonostyli, lateral.

Type locality.—“Vicinity of Port Western” (?=Western Port), Vic.

Type location.—Unknown.

Distribution.—QUEENSLAND: Stanthorpe. NEW SOUTH WALES: Bathurst, Ben Lomond, Blackheath, Blundell's (A.C.T.), Bombala, Bungendore, Cooma, Countegany, Forest Reefs, Glen Innes, Hall (A.C.T.), Hotel Kosciusko, Koorawatha, Lawson, Moss Vale, Mt. Gingera,

5500 ft. (A.C.T.), Mt. Victoria, Orange, Queanbeyan, Sydney, Tubrabucca, Uralla. VICTORIA: Benonijsfield, Broadford, Buchan, Croydon, Heathcote Junction, Jamieson Valley, Jerrama, Mansfield, Melbourne, Mt. Macedon, Port Phillip, Ringwood, Tyabb, Wallan, Woori Yallock. TASMANIA: Hobart, Launceston, Melton, Ouse, Triabunna, Waterhouse Estate.

The species is extremely variable in size, in the shape of the fore tibial teeth, and in the dorsal outline of the pronotum; also the degree of convexity and the denseness of vestiture of the pygidium. It seems likely that it includes a large number of infra-subspecific forms, but owing to lack of adequate labelling of most specimens it is not possible to study these differences in relation to distribution.

27. ANOPLOGNATHUS HIRSUTUS Burmeister

Figs. 69-71

Anoplognathus hirsutus Bermeister, 1844, Handb. Ent. 4 (1): 447; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 112.

Anoplognathus hirsutus var. *quadraticeps* Ohaus, 1904, op. cit. 65: 113.

Anoplognathus explanatus Arrow, 1901, Ann. Mag. Nat. Hist. (7) 7: 397 (syn. nov.).

This species is very closely related to *suturalis* Boisd. The form described by Arrow is merely an extreme colour variant; its purple lustre is characteristic of individuals that have spent their larval stages in unusually damp situations. Such specimens can be obtained by rearing *hirsutus* larvae in the insectary under conditions of excess moisture. The prominent elytral costa and the pear-shaped outline mentioned by Arrow are not peculiar to this form. Ohaus refers to a difference in the form of the male genitalia but the present author can discern no significant differences between the genitalia of the two forms.

♂. Length 18-22.5 mm. ♀. Length 21-23.5 mm.

From *suturalis* the present species differs as follows: Body colour generally darker, clypeus slightly less dilated at apex; pronotum much more abundantly clothed, with the basal angles usually bearing white hairs, anterior angles more acute; elytra apices individually rounded and producing a wide re-entrant angle; male genitalia (Figs. 70, 71) differing markedly in structure.

The species is extremely variable in colour, vestiture, and in the degree of curvature of the male pygidium. In addition to the most common form, what appear to be infra-subspecific forms are recognized from two localities:

Kosciusko form: 4 ♂♂ and 1 ♀ from the Chalet area are a distinctly darker reddish brown in body colour, with much reduced dorsal vestiture, the pygidium being almost glabrous.

Ben Lomond form: 2 ♂♂ from this locality are dark, as in the previous form, but have a normal degree of vestiture on the dorsal surface.

Type locality.—Unknown.

Type location.—Unknown.

Distribution.—QUEENSLAND: Stanthorpe. NEW SOUTH WALES: Armidale, Blue Mountains, Braidwood, Bombala, Canberra (A.C.T.), Cooma, Ebor, Forest Reefs, Glen Innes, Guyra, Jindabyne, Monaro, Mt. Kosciusko, Tamworth, Uralla. VICTORIA: Bacchus Marsh, Box Hill, Bruthen, Buxton, Cobungra, Glen Wills, Healesville, Heathcote Junction, Heathmont, Kerrisdale, Lal Lal,

Launching Place, Macedon, Nunawading, Olinda, Phillip I., Warburton, Woori Yallock, Yarra Junction. Ohaus refers to examples from Queensland, Sydney, and Mansfield, Vic.

Dates of collection.—November (Qld.) to March (Vic.).

Specimens examined.—24 ♂♂, 26 ♀♀.

28. ANOPLOGNATHUS RUBIGINOSUS Macleay

Fig. 72

Anoplognathus rubiginosus Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 358; Ohaus, 1904, Stettin, ent. Ztg 65: 103.

It seems certain that Ohaus misidentified this species as he placed it between *odevahni* and *nebulosus* and referred to its clypeus being similar to that of *boisdurali*. Specimens from the type locality in the Macleay Museum (designated as types by the present author) are widely different from these three species, and obviously belong to the *suturalis* species group. It is very close to *suturalis* and might be more properly regarded as a form of this extremely plastic species. However, very few specimens were available for study, and no change in status is made here.

Dark reddish brown with green or violet reflections.

♂. Length 19–21.5 mm. From *suturalis* it differs in its dark reddish brown colour; clypeus (Fig. 72) bearing short and barely discernible pale brown hairs, these restricted to clypeus and ocular margins of frons. Ocular canthi and thorax with yellowish grey villosum. Pronotum quite glabrous; abdomen black; pygidium with a deep green sheen, bearing much shorter erect white hairs. Mesosternal process much more elongate, slender, and sharp, its apex overhanging mid fore coxae. From *hirsutus*, it differs in having contiguous elytral apices, and in the form of its ♂ genitalia, which are of the *suturalis* type.

♀. Length 21–23.5 mm. The pronotum is markedly more convex than that of *suturalis*, and the anterior angles are distinctly obtuse.

Type locality.—New England district of New South Wales.

Type location.—♂ holotype and ♀ allotype in MACL.

Distribution.—NEW SOUTH WALES: Tenterfield, Uralla.

Dates of collection.—None known.

Specimens examined.—♂, ♀ types, 4 other ♂♂.

Collections.—CSIRO; MACL.

29. ANOPLOGNATHUS PARVULUS Waterhouse

Figs. 76, 77

Anoplognathus parvulus Waterhouse, 1873, Ent. Mon. Mag. 10: 75; Ohaus, 1898, Stettin, ent. Ztg 59: 37; 1904, op. cit. 65: 118.

Calloodes mastersi Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 360.

Anoplognathus mastersi Olliff, 1890–91, Rec. Aust. Mus. 1: 72.

Anoplognathus parvulus var. *cuprifulgens* Ohaus, 1904, Stettin, ent. Ztg 65: 119.

This species is identified in most collections as *C. mastersi* MacL. Olliff (1890–91) was the first to recognize its misplacement in this genus, writing “*C. mastersi* Macleay has the anterior tibiae armed with spines like those of *A. punctulatus* and *C. prasinus*. I am, therefore, inclined to refer all these species to *Anoplognathus*, as true *Calloodes*

has edentate anterior tibiae." Types of *mastersi* have been selected from material labelled "Port Denison" in the Macleay Museum collections. The colour variety described by Ohaus is fairly common and all intergrades between the typical yellowish green and the red forms are found. A third colour form of this species is a metallic brown that corresponds to the *concinus* form of *aureus*; extreme variants always have some trace of green remaining, at least on the metepisterna.

Golden green species, sometimes with roseate reflections on dorsal surface; rarely a concolorous dark glossy brown; mouthparts and legs reddish brown, base of mentum and abdominal sternites green.

♂. Length 16–18 mm. Clypeus with sides concave in dorsal profile, at first narrowing, then dilated at gently recurved anterior margin; apical truncated face deep, lightly setose; head with sparse short erect hairs, absent from or sparse on frons, with confluent irregular punctures becoming discrete towards vertex; clypeo-frontal suture transverse, dark; ocular canthi bearing white setae.

Pronotum and scutellum with fine but distinct dense punctuation, the former with sides rounded or slightly contracted behind anterior angles, the ridges continuous or just obsolete across middle, the basal margin forming a simple median lobe sometimes with a slight median indentation.

Elytra with fairly distinct striae of fine punctures. Epipleurae with a weak coppery sheen, glabrous, weakly serrate near apices, the latter contiguous but not squarely cut.

Fore tibiae weakly microreticulate, broad, abundantly clothed with fine pale brown hairs, basal tooth subobsolete, the other teeth well developed and at a wide angle to axis of tibia. Postcoxal prosternal process present, bearing white setae. Hind legs slender, femora almost glabrous; tibiae with pale brown hairs, distinctly bicarinate, spurs separated by 2 or 3 fine ciliae.

Mesosternal process flat, glabrous, golden green with dark diffuse pigment on sutures, apex broadly rounded and scarcely surpassing mesocoxae, lightly punctate on mid line, coarsely so at sides. Abdominal sternites glabrous across middle, the last segment reddish brown with green patches.

Propygidium with caudal margin brown and overlaid by short decumbent white hairs; pygidium flat, with dense irregular confluent punctuation, with sparse short white hairs and longer pale reddish brown hairs near apical ridge, the sides compressed. Genitalia as in Figures 76, 77.

♀. Length 16–19·5 mm. Clypeus with all margins evenly recurved; elytra with apices more squarely cut than in ♂; fore tibiae distinctly 3-dentate. Larger fore tarsal claws toothed. Last abdominal sternite somewhat excised in middle of hind margin.

Type localities.—*parvulus*: eastern Australia; *mastersi*: Port Denison, Qld.

Type locations.—*parvulus*: BM; *mastersi*: MACL (holotype ♂ and allotype ♀ selected by present author).

Distribution.—QUEENSLAND: Ayr, Bowen, Brisbane, Cairns, Coen, Gayndah, Herbert R., Innisfail, Johnston R., Port Denison, Mackay, Richmond, Rockhampton, Sarina, Sunnybank.

Dates of collection.—December to April.

Specimens examined.—14 ♂♂, 14 ♀♀.

30. ANOPLOGNATHUS ANTIQUUS Arrow

Figs. 82, 83

Anoplognathus antiquus Arrow, 1919, Ann. Mag. Nat. Hist. (9) 4: 382, pl. 8, figs. 2, 3.? *Trioplognathus griseopilosus* Ohaus, 1901, Dtsch. ent. Z. 1901: 130.

The author has examined the type pair of Arrow's species. There is remarkably close agreement between them and the description of *griseopilosus* Ohaus, and the two may prove to be synonymous. As the description of the latter species is inadequate, a decision must await the location and examination of the type. The author has no doubt that *antiquus* is correctly placed in *Anoplognathus*.

The striking resemblance of this species to *velutinus* Boisd. has been pointed out by Arrow. Examination of the male genitalia and the mesosternal process suggest that it is most closely allied to the *parvulus* and *brunnipennis* species groups.

Yellowish brown species with abundant adpressed white scale-like hairs on dorsal surface; eyes, head, pronotum, and humeral calli bearing dark brown markings. Underside reddish brown, with abundant long white or pale yellow hairs.

♂. Length c. 22 mm. Clypeus (Fig. 83) of the *brunnipennis* type, depressed at sides behind recurved anterior margin; apical truncated face and disc of clypeus setose; clypeofrontal suture bisinuate, the median node extended on frons as a median impunctate stripe. Head with fine confluent punctation on clypeus, the punctures larger on frons and becoming discrete near vertex. Ocular canthi with dense pale yellow setae.

Pronotum quite strongly convex, anterior angles not produced and rather blunt, sides evenly rounded, the ridges with a greenish stain; basal ridge obsolete across simple median lobe; disc with punctuation quite coarse in middle, becoming denser towards margins; micropunctures present. Scutellum with large punctures bearing white adpressed hairs, the margins dark brown with a greenish sheen.

Elytra with epipleurae weakly serrate towards apices, the latter contiguous, squarely cut, and rising abruptly to subapical calli; disc with punctures finest near sutural margins, each bearing a single white hair.

Fore tibiae abundantly clothed with white hairs, 3-dentate but with the basal tooth small, the others short and stubby; hind femora abundantly clothed; tibiae with both hairs and dark ciliae, spurs separated by 3-4 fine ciliae.

Mesosternal process abundantly setose, broad, flat, apex rounded and scarcely surpassing mid coxae.

Pygidium confluently punctate, transversely rugulose, with dense adpressed white hairs and sparse yellowish apical hairs; abdomen reddish brown, densely clothed. Genitalia as in Figure 82.

♀. Length c. 24 mm. Clypeus rounded, clypeofrontal suture more transverse. Epipleurae not serrate; fore tibial teeth deeper and more acute, the larger claws toothed. Pygidium with apex produced and ridge obsolete.

Type locality.—Richmond R., N.S.W.

Type location.—♂ and ♀ types in BM.

Specimens examined.—Types.

31. ANOPLOGNATHUS BRUNNIPENNIS Gyllenhal

Figs. 84, 85

Rutela brunnipennis Gyllenhal, 1817, in Schöenherr, Syn. Ins. 1 (3), app. p. 62.*Anoplognathus brunnipennis* Boisduval, 1835, Voy. Astrolabe, Col. 2: 175; Macleay, 1873, Trans. Ent. Soc. N.S.W. 2: 355; Ohaus, 1904, Stettin. ent. Ztg 65: 115.*Anoplognathus flavipennis* Boisduval, 1835, Voy. Astrolabe, Col. 2: 176 (syn. nov.).*Anoplognathus castaneipennis* Laporte, 1840, Hist. Nat. Col. 2: 126.*Anoplognathus quadrimaculatus* Ohaus, 1898, Stettin. ent. Ztg 59: 34; 1904, op. cit. 65: 116 (syn. nov.).

Examination of extensive material has shown that the forms identified as *brunnipennis* Gyll. and *flavipennis* Boisd. are colour variants of the same species. The name *quadrimaculatus* Ohaus applies to lighter-coloured individuals in which the humeral and subapical calli are pigmented. Ohaus (1904) states (in transl.) ". . . I find that in *quadrimaculatus*, in addition to the brown humeral and subapical calli, the sides of the prothorax are invariably strongly punctate and hairy, whereas in *flavipennis* they are invariably bare . . ." The present author finds no such difference in the specimens before him. Specimens of both kinds, and intermediates, are found coexisting in field populations.

Head, pronotum, and scutellum green, or reddish brown with dark green areas, always with a golden green sheen. Elytra variable in colour, ranging from pale biscuit to deep red-brown, the lighter forms sometimes retaining darker pigment on the elytral calli. Legs light to deep red-brown, tarsi almost black with a green sheen; mesosternum deep green, abdomen and pygidium red-brown with a green sheen.

♂. Length 18–20.5 mm. Clypeus of the *punctulatus* type, the sides concave in dorsal profile, finely emarginate and strongly deflexed before recurved anterior margin; apical truncated face and disc densely clothed with erect white hairs. Ocular canthi and frons bearing similar hairs. Head closely and irregularly punctate, with abundant micropunctures; clypeofrontal suture bronze, transverse.

Pronotum weakly convex, sides slightly angulate and contracted behind produced acute anterior angles; basal angles well defined; both anterior and basal ridges subobsolete across middle, basal margin with a simple median lobe; disc with a faint median impressed line, finely and sparsely punctate, with a pair of lateral impressions. Scutellum lightly punctate.

Elytra with white humeral hairs; epipleurae with white hairs and slight serrations near apices; the latter contiguous but not squarely cut; disc slightly compressed behind humeral calli, with fine punctures underlain by minute pigmented spots (obscured in dark specimens).

Fore tibiae broad, shallowly toothed, bearing white hairs. Hind legs slender, lightly clothed, tibiae with stout dark ciliae, spurs separated by 2 fine ciliae.

Mesosternal process flat, setose at sides, apex broadly rounded, extending only half way to fore coxae; postcoxal prosternal process present, truncate and bearing white bristles. Abdomen with sparse erect and shorter decumbent white hairs across all sternites.

Pygidium bearing dense clothing of white hairs, with longer pale yellow hairs near and on apical ridge; disc slightly convex in profile. Genitalia as in Figures 84, 85.

♂. Length 19–21 mm. Head finely and evenly emarginate, rounded, disc more coarsely and heavily punctate, vestiture inconspicuous, with short erect pale hairs present on clypeus and ocular margins of frons. Fore tibiae slender, teeth acute and deeply separated, the apical tooth prolonged; larger fore tarsal claws toothed. Pronotum with anterior angles not produced, sides more evenly rounded. Elytra with strong flaring over metacoxae.

Type locality.—*quadrimaculatus*: "Queensland". Others unknown.

Type locations.—Unknown.

Distribution.—QUEENSLAND: Ayt, Fletcher, Gympie, Herberton, Innisfail, Mackay, Stanthorpe, Toowoomba, Warea. NEW SOUTH WALES: Belmont, Blue Mountains, Dalwood, Gosford, Inverell, Maitland, Port Jackson, Singleton, 50 miles S. of.

Date of collection.—September (N. Qld.) to January (N.S.W.).

Specimens examined.—26 ♂♂, 26 ♀♀.

32. ANOPLOGNATHUS DAEMELI Ohaus

Figs. 78–81

Anoplognathus daemeli Ohaus, 1898, Stettin, ent. Ztg 59: 34; 1904, op. cit. 65: 117.

Anoplognathus daemeli var. *mixtus* Ohaus, 1898, op. cit. 59: 35; 1904, op. cit. 65: 118.

Head, thorax, and scutellum bright metallic green suffused with coppery red on margins of head; pygidium, abdomen, and mesocoxae green or reddish brown with a green sheen; coxae and abdomen with abundant short white or greyish hairs.

♂. Length 17–20 mm. Clypeus transverse, strongly narrowed towards apex, sides slightly convex in dorsal profile and finely emarginate; anterior margin with narrow but very abrupt median elevation (Fig. 80), anterior truncated face sparsely setose; disc glabrous, confluent punctate or rugulose, surface depressed towards anterior angles; clypeofrontal suture a fine bisinuate coppery line; frons discretely punctate except adjacent to suture, bearing abundant micropunctures; ocular canthi bearing white setae; eyes protuberant.

Pronotum with sides markedly contracted behind acute anterior angles, basal margin with a simple median lobe, the ridge obsolete in the middle; disc with very fine but rather dense punctuation, often with a well-defined median impressed line.

Elytra reddish brown with patches of darker pigment anteriorly, margins deep reddish brown with green sheen; epipleurae bearing sparse setae, moderately serrate, apices contiguous but not squarely cut, disc with small fine punctures forming distinct striae, the surface slightly compressed behind humeral calli.

Fore tibiae with abundant hairs, 3-dentate, the teeth shallow and the basal tooth small, first segments of tarsi elongate. Hind legs slender, well clothed, tibial spurs separated by 2 fine ciliae.

Mesosternal process (Fig. 81) flat, setose in middle behind apex, the latter evenly rounded, extending barely half way to fore coxae. Postcoxal prosternal process present. Abdomen sparsely clothed on mid line.

Propygidium with conspicuous caudal fringe of white hairs; pygidium bearing similar hairs over whole surface, also with pale reddish brown hairs behind narrow but well-defined apical ridge; disc slightly convex in profile. Genitalia as in Figures 78, 79.

♀. Length 17–22 mm. Antennal club shorter; clypeus without anterior elevation; elytral apices rather more squarely cut; fore tarsi with larger claws strongly toothed; pygidium slightly less convex.

Type locality.—Innisfail, Qld.

Type location.—Unknown.

Distribution.—QUEENSLAND: Byfield, Gordonvale, Innisfail, Port Mackay (type locality of var. *micantipennis*), Port Denison.

Dates of collection.—None known.

Specimens examined.—3 ♂♂, 7 ♀♀.

Collections.—AM; MACL; NM; QM.

The species is variable in size. A male and two females from Byfield are smaller and the male less strongly armed than those from Port Denison, but their females show no structural differences. The latter sex may be confused with females of *brunnipennis* but differ in their complete lack of elytral flaring and in their relatively broader head.

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REVISION OF THE GENUS ANOPLOGNATHUS LEACH



Beetles (*Anoplognathus montanus* MacL.) defoliating *Eucalyptus rubida* Deane & Maid. near Hall,
A.C.T., January 1950.

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